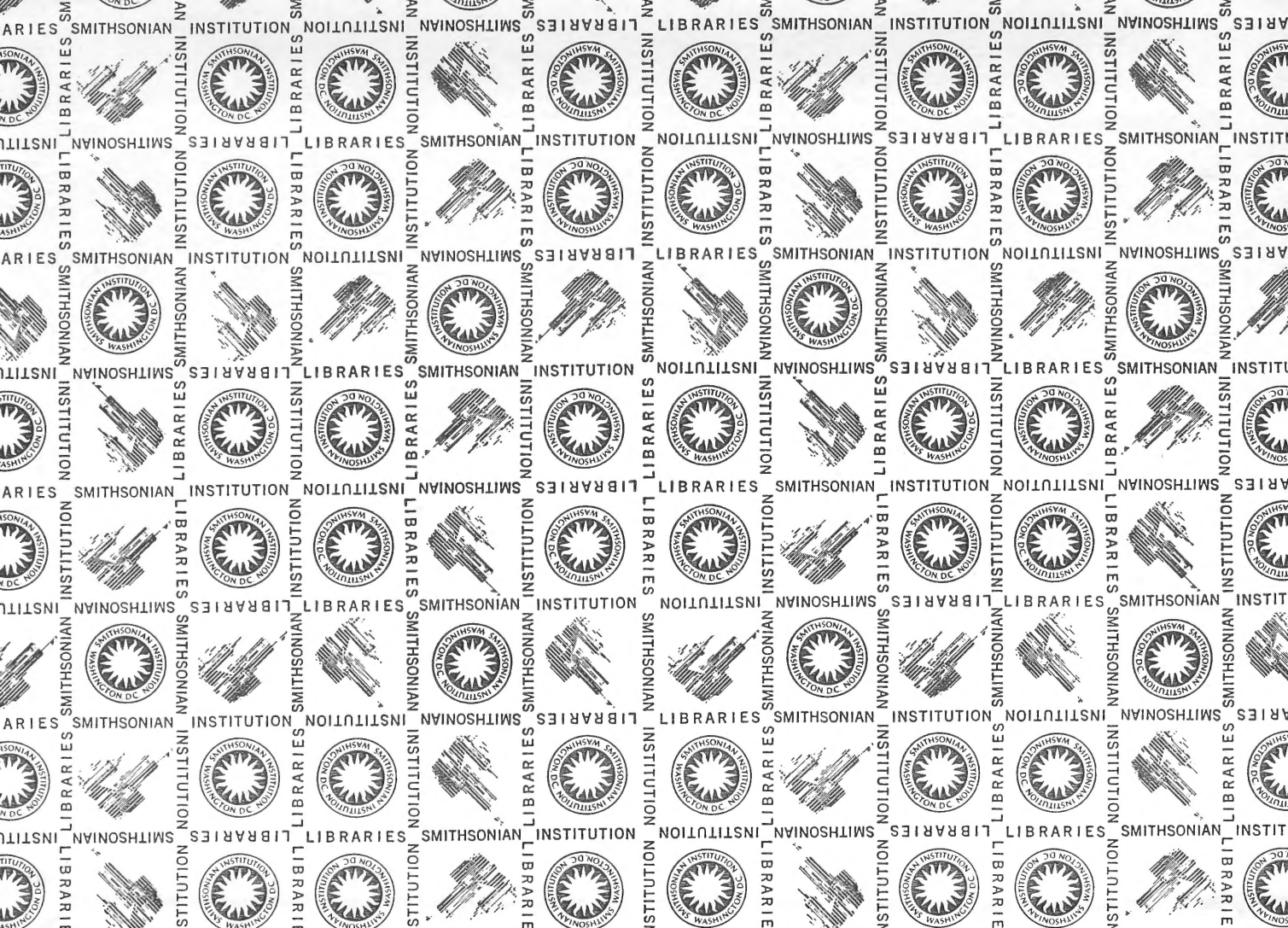
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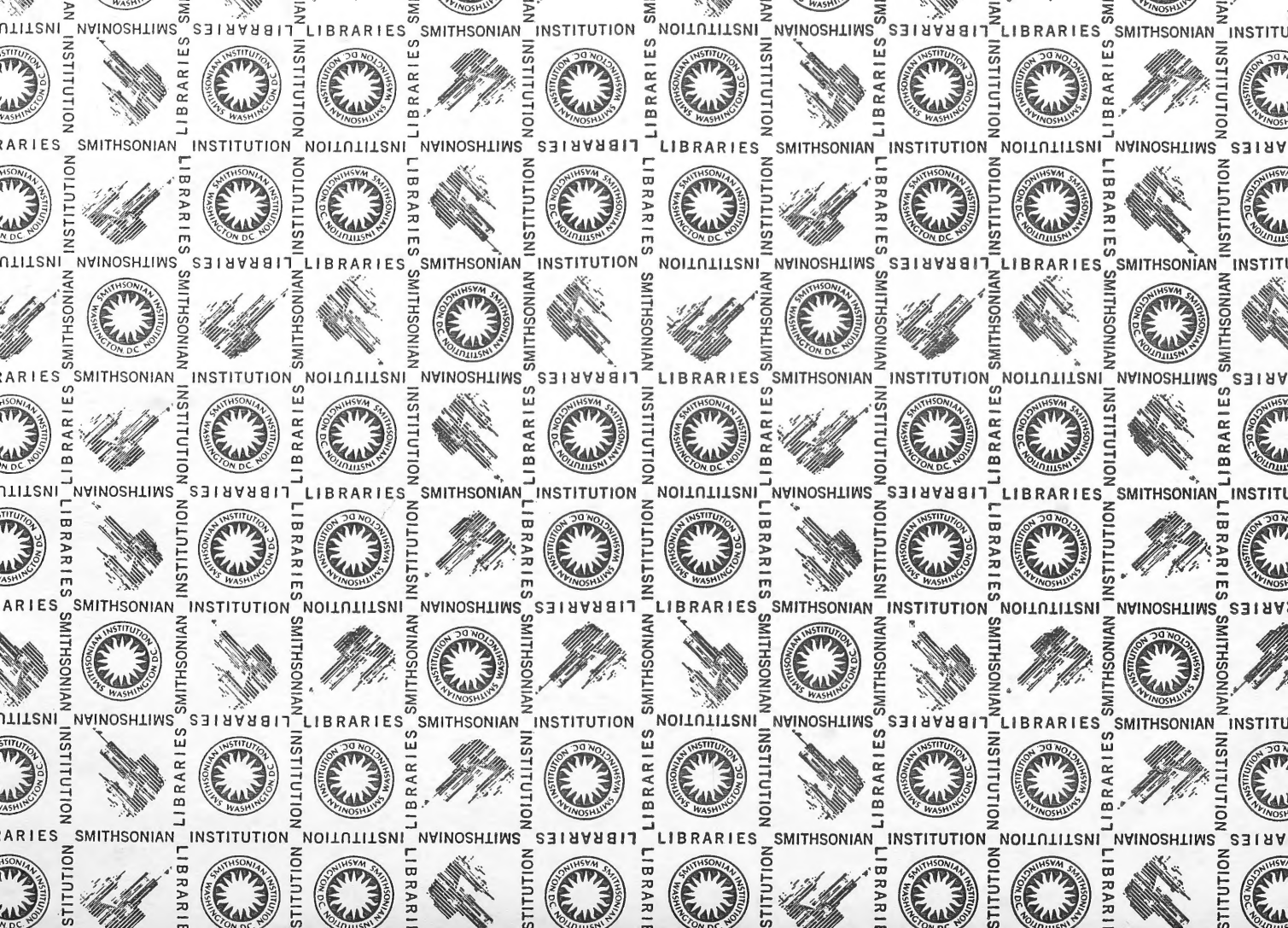
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Population Status of California Sea Otters

Population Status of California Sea Otters
Pacific OCS Region
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Population Status of California Sea Otters

Edited by

D. B. Siniff
Department of Ecology and Behavioral Biology
University of Minnesota
Minneapolis, MN 55455

and

K. Ralls
National Zoological Park
Smithsonian Institution
Washington, D.C. 20008

November 30, 1988

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Model

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ABSTRACT

The main objective of the contract was to develop a simulation model to facilitate analysis of the risk of oil spills to the threatened California sea otter population. Existing data on the dynamics and demography of the population were reviewed and synthesized. The additional data needed for model development were collected through radiotelemetry studies of sea otters in Alaska and California.

Our field work indicated that the California population had a high reproductive rate but many pups did not survive to weaning. Adult females had the highest survival rates and adult males the lowest. Juvenile females had lower survival rates than adult females and spent more time foraging than other otters. Otters tended to stay within a small area for an extended period and then suddenly move for a considerable distance. They made more long-distance movements than expected. Juvenile males tended to travel more extensively and range farther offshore than other otters.

The simulation model contains four interrelated stochastic submodels: a short-term population model, a long-term population model, a sea otter distribution model, and a sea otter movement model. This report includes a detailed description of the model, the data on which it is based, and an operating manual. The computer program for the model has also been provided to MMS.

TECHNICAL SUMMARY

Chapter 1.

The objectives of the contract were to review and synthesize existing information on the dynamics and demography of the threatened California sea otter population, to design and conduct field studies to collect the data needed to fill data gaps identified through this process, and to develop a simulation model to facilitate analysis of the risk of oil spills to this population.

We computerized past survey data collected by the California Department of Fish and Game and the U.S. Fish and Wildlife Service and aged teeth from the salvaged otters found dead along the California beaches over the last 20 years.

The additional data needed for model development were collected through radiotelemetry studies of sea otters in Alaska and California. Because of the sensitive nature of hands-on field work on the threatened California population, we tested procedures and equipment in Alaska before applying for permits to use them in California. We developed and used a radio transmitter that could be implanted within the abdominal cavity of sea otters. The use of these transmitters enabled us to make a number of new discoveries about sea otters in both Alaska and California.

Chapter 2.

We observed 40 California sea otters, representing all four major age/sex groups, that were flipper-tagged and instrumented with implanted radio transmitters.

The proportion of females accompanied by a pup peaked in the spring, with a secondary peak in the fall. Two methods of estimating the annual reproductive rate gave comparable values of 0.88 and 0.90 pups per adult female. The average inter-birth interval was 416 days. Eight of the 19 pups born did not survive to weaning.

Among the four major age/sex classes, adult females had the highest estimated survival rates and the adult males the lowest. Juvenile females had lower survival rates than adult females but juvenile males had higher survival rates than adult males.

The estimated annual loss rate for the flipper-tags was 0.26. More individuals lost two tags than would be expected by chance. It is unlikely that accurate estimates of sea otter survival rates can be derived from observations of tagged individuals.

Chapter 3.

We obtained a detailed picture of sea otter movement patterns in California by attempting to locate each instrumented otter, by radiotelemetry, on a daily basis. In general, otters tended to stay within a small area (1-2 km of shoreline) for an extended period and then suddenly move for a much longer distance. Our daily monitoring revealed that individual otters of all age/sex classes make a surprising number of long-distance movements at all times of year. There was substantial variation in movement patterns among individuals within all age/sex classes but there were also significant differences between classes. Juvenile males were the most extensive travelers and also ranged farther offshore than otters of the other age/sex classes.

Chapter 4.

Radiotelemetry is particularly useful for collecting time budget and activity data on sea otters because radio signals are not transmitted through sea water. Three general categories of activity can be distinguished by listening to the radio signal from an otter: resting, feeding, and "other". Otters of all age/sex classes tended to be active and feed for a large proportion of the time during the late afternoon and early evening but there were differences in the activity patterns of the various groups. Juvenile females and adult females with pups spent more time foraging than other otters. Differences in the ability of members of different age/sex classes to compete for food resources are common in vertebrates. In the California sea otter population, the juvenile females spent almost half of their time foraging, suggesting that they are poor competitors for food.

Chapter 5.

Although we collected some data on uninstrumented otters, we focused on the foraging patterns of individual instrumented sea otters as indicated by radio-telemetry. Our telemetry data indicated that visual observations of otter foraging patterns tend to underestimate mean dive lengths. There was a striking degree of individual variation in foraging patterns. Many individuals displayed differences in diurnal and nocturnal dive-length patterns that may reflect a tendency to specialize on different prey species by day and night. However, there was no general tendency for longer dive lengths or surface intervals during the day or night. Juvenile males often fed far from shore where they could not be seen. Juvenile females had longer feeding bouts than otters of the other age/sex classes.

Chapter 6.

In an effort to gain insight into the age structure of the California population, we studied a sample of premolars from more than 580 dead sea otters salvaged from beaches. We counted bands in the cementum of the sectioned teeth to estimate age. We were able to examine teeth from ten otters of known minimum age and the age estimates based on these teeth compared quite favorably with those made by field biologists. Age estimates based on teeth also compared well with those based on skull features. Teeth that had been boiled were more difficult to interpret than those that had not been boiled. There was excellent agreement between successive age estimates by the same reader and good agreement across readers.

Chapter 7.

We evaluated the accuracy and precision of the radiotelemetry methods we used to locate otters in California with a radio transmitter on a buoy anchored off the coast. We established the location of the buoy with visual methods and took a series of compass bearings on the buoy's radio signal. Signal bounce was not a significant problem. The accuracy of our bearings compared quite favorably with that of those taken in other radio-telemetry studies. For otters located within about 800 meters from shore, precision was estimated at 0.03 to 0.06 hectares and accuracy at 51 to 110 meters. The results obtained by hand-plotting points, which was our usual field procedure, compared well with those obtained with the Andrews estimator calculated by the computer program TRIANG.

Chapter 8.

This chapter focuses on relatively long-term movement patterns of adult female and juvenile sea otters in Alaska. Adult females were much more mobile than had previously been suspected but their movements were greatly reduced in the month before weaning. Male weanlings left the area in which they were born shortly after weaning, so that spatial segregation of the sexes occurred at a very young age. Sea otters used different portions of the available habitat for different purposes, such as for weaning pups and over-wintering. Hence, movements and habitat use varied seasonally.

Chapter 9.

Birth dates, growth rates, dependency periods, weanling behavior and survival of male and female otter pups in Alaska

were compared. Many of these factors did not vary between males and females. However, dependent male pups grew more rapidly than dependent females and weaned females had lower survival rates than weaned males.

Chapter 10.

A stochastic simulation model of California sea otter population dynamics was constructed to be used in the analysis of the risk of oil spills to the legally threatened population. The model consists of four submodels: 1) a population model that iterates on a monthly basis; 2) a population model that iterates on a yearly basis; 3) a spatially explicit population distribution model; and 4) a sea otter movement model. Simulated population dynamics are density-dependent but the model has the flexibility to allow investigation of density-independent reproduction and mortality. The monthly population submodel operates for four simulated years before the simulated oil spill. At the time of the spill, individual animals are distributed along the coast by the distribution submodel. In the movement submodel, individual animals then either avoid or are killed by the spill. Population recovery can be simulated for up to 50 years after the spill using the monthly and annual population models.

Age and sex specific survival and reproductive rates are the core of the population submodel. These rates are estimated using telemetry and other data in a "competing risks" theoretical framework. Data from the semi-annual censuses of the population conducted by the California Department of Fish and Game and the U.S. Fish and Wildlife Service are incorporated in the distribution model. In the movement submodel, daily movements are modeled with regression equations, using parameters estimated from the radiotelemetry data on the California animals.

Sensitivity analysis of the population model indicated that the recovery time after a spill depends on the percentage of the female population killed, the status of the population in relation to its carrying capacity at the time of the spill, and the amount of environmental stochasticity in annual survival rates.

CHAPTER 1

OVERVIEW OF THE STUDY: BACKGROUND AND GENERAL METHODS

D. B. SINIFF AND K. RALLS

November 30, 1988

BACKGROUND

The outer continental shelf of the Pacific coast is believed to contain extensive oil and gas reserves. The Santa Maria and Santa Cruz Basins, off the coast of central California, are potentially some of the most active areas of oil exploration and development. Areas to the south of Point Conception have already been developed into productive fields, and more will be developed in the future. The Minerals Management Service (MMS), U.S. Department of Interior, is the federal agency responsible for administering leases of submerged federal lands. Amendments to the Outer Continental Shelf Lands Act of 1953 set MMS objectives for managing development of outer continental shelf lands, including protection of human, marine, and coastal environments.

A first step in making decisions about leasing, exploration, and development that protects the marine and coastal environment is risk analysis. MMS has directed and funded a number of studies of the risk of off-shore oil development, particularly of oil spills resulting from leasing activities, to wildlife populations (e.g. Ford 1985, Reed, et al., 1986).

One of the most sensitive wildlife species, from both political and biological perspectives, that could be impacted by an accidental spill development in the Santa Maria and Santa Cruz Basins is the California sea otter (Enhydra lutris). Commercial exploitation during the 18th and 19th centuries reduced the aboriginal population of perhaps 20,000 otters along the California coast to probably less than 100 in 1911 (USFWS 1986). Protection provided by international treaty and federal and state legislation allowed the population to recover, at a rate of about 5% per year, to its present size of approximately 1500 animals (Ralls, et al., 1983). In 1976 the southern sea otter was officially listed as "threatened" under the Endangered Species Act; a major reason for the designation was the potential risk of oil spills to the small and geographically isolated population. To obtain information on the southern sea otter, MMS issued a request for proposal in late April 1983. It outlined a series of objectives for studies on "The Population Status of California Sea Otters". Three objectives were central to this request for proposal: 1) to consider the existing information on the dynamics and demography of the California sea otter population and determine what additional information would be necessary to predict the effects of oil spills, of various sizes in different parts of the sea otter range in California (Fig. 1.1), on the population; 2) to design and conduct studies needed to fill the identified data gaps; and 3) to develop a population model that would help to determine the way in which the size and productivity of the population would

be likely to be affected by oil spills in different parts of the range.

In October, 1983, we received the contract to carry out this work and immediately started to obtain the necessary federal and state permits to conduct field studies of sea otters in California. We proposed the use of implanted radio transmitters to monitor otters along the California coast. In March, 1984, we received the necessary permits to implant five otters and began field work in California. We subsequently obtained additional permits and have implanted a total of 40 sea otters in California and monitored them through late December, 1987. In this report, we analyze the data collected on these individuals and the results are presented in Chapters 2 through 5.

We collected teeth from the salvaged otters found dead along the California coast over the last 20 years. The teeth were sectioned to allow estimation of the ages of individuals. This information was used in the development of the population model. The methods used and the results of the tooth analysis is presented in Chapter 6. In the development of the model, the data from the field studies were used primarily for establishing a basis for movement patterns along the coast and estimates of reproduction and survival rates. Since the precision and accuracy of the telemetry positions along the California coast were important in our analyses, an evaluation was carried out using transmitters at fixed locations that simulated floating otters. This evaluation is presented in Chapter 7.

Because the California sea otter population is classified as threatened under the Endangered Species Act, we tested procedures and equipment on sea otters in Prince William Sound, Alaska (Fig. 1.2), before using them in California. Data on sea otters in Alaska were collected while equipment and procedures were being developed. These data resulted in significant new findings, particularly with respect to events during the period of pup dependency. They are presented in two chapters of this report, "Movement patterns of adult female and weanling sea otters in Prince William Sound, Alaska" (Chapter 8) and "Sex-related patterns in the post-natal development and survival of sea otters in Prince William Sound, Alaska" (Chapter 9).

The final chapter of this report describes the population model that we developed. A significant body of data from diverse sources has been integrated into this effort. These data have come from our current field studies as well as the

FIGURE 1.1 - A map of the study area in California showing the approximate range of sea otters during the period of the study in 1984, 1985, and 1986. The portion of the range in which reproduction occurs is indicated by cross-hatching; the northern and southern areas occupied mostly by males are indicated by diagonal lines.

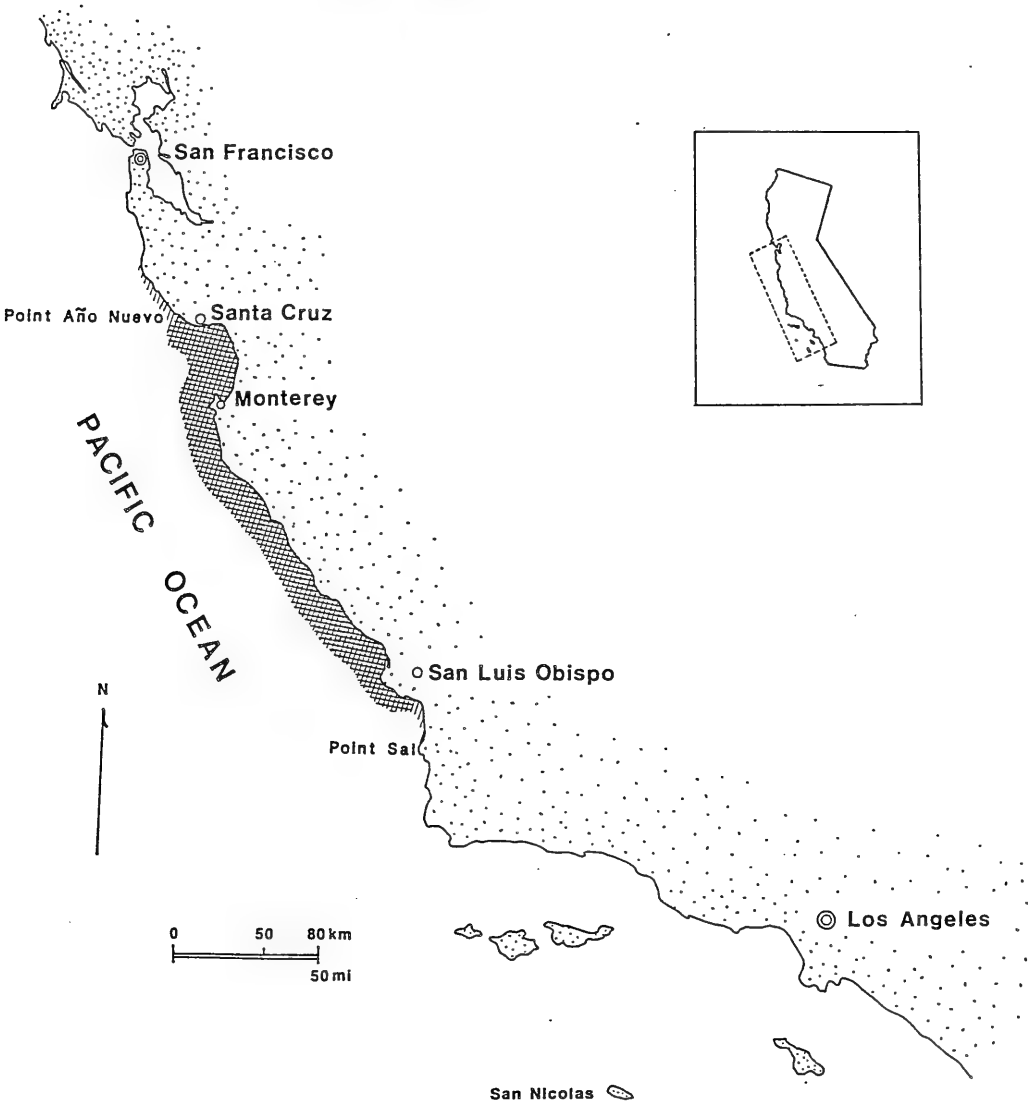
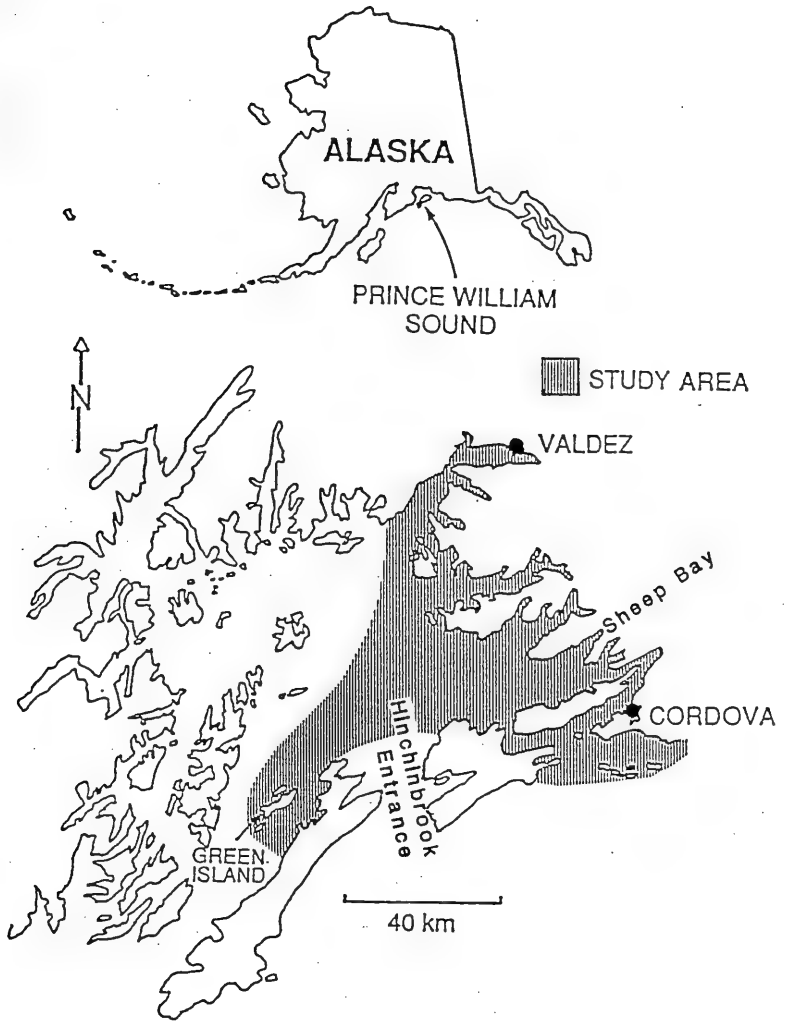


FIGURE 1.2 - A map of the study area in Alaska showing the general range of the sea otters that were studied during 1984 and 1985.



past efforts of both the California Department of Fish and Game and the U.S. Fish and Wildlife Service. We organized all these past survey data into a data base and used it extensively in the development of the model.

GENERAL METHODS

Capture and release

We captured otters in three ways: with floating gill-nets, the Wilson trap developed by the California Department of Fish and Game (Ames, et al., 1983), and dip-nets, which have been used extensively by the U.S. Fish and Wildlife Service in California. Floating gill-nets were used mostly in Alaska. We used them initially in California but wind and fog made it difficult to check the nets frequently. The majority of the adult otters in California were captured with the Wilson trap and most of the juveniles with dip-nets. We also used dip-nets to capture pups and newly independent young in Alaska. All animals were released near the point of capture.

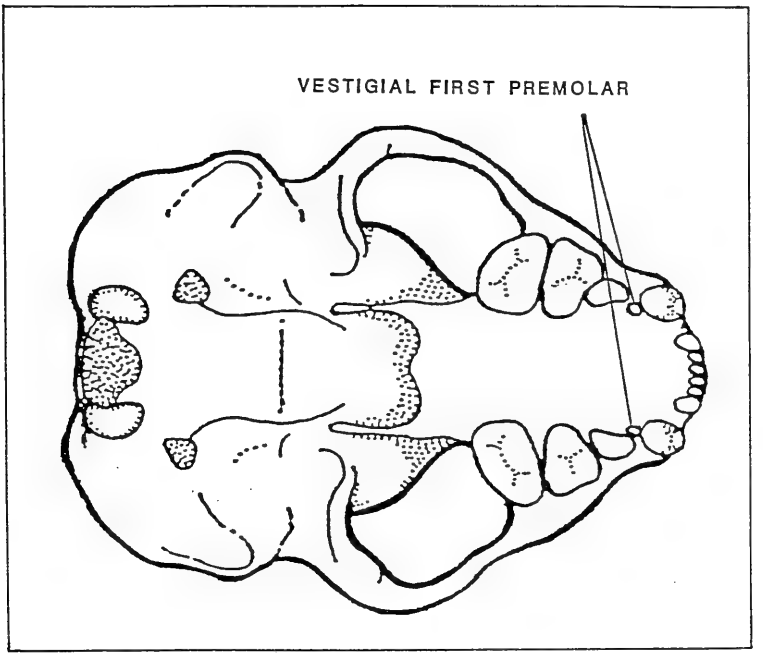
Teeth

Sea otters have a small, vestigial premolar directly behind each canine (Fig. 1.3). Schneider (1973) developed an aging technique based upon the number of cementum layers found in stained sections and Garshelis (1984) applied this technique to teeth extracted from anesthetized sea otters in Alaska. We collected this premolar from many of the California animals. However, our sample was incomplete due to lack of permission to extract a tooth during the early portion of the study and some breakage during extraction of the teeth.

Transmitters

The transmitters were developed by the University of Minnesota's Cedar Creek Bioelectronics Laboratory. The first models, used in Alaska in 1982 before this project began, measured about 6.8 x 4.8 x 1.8 cm and weighed about 70 g. Although it had been shown that implanting transmitters in the abdominal cavity had no deleterious effects in other species (Smith, 1980; Eagle, et al., 1984), no information on this point was available for sea otters. Therefore we set out to compare the results of implanting transmitters beneath the skin (subcutaneous) and within the abdominal cavity

FIGURE 1.3 -- Schematic drawing of the upper jaw of a sea otter showing the vestigial first premolar that was sometimes removed from captured animals and sectioned for determination of age.



(intraperitoneal). Because some of the 1982 implants were to be subcutaneous, we used small, flat batteries on which we had no previous performance data. Neither method of implantation appeared to have significant deleterious effects on the otters; however, the subcutaneous implantation procedure left a noticeable lump so we decided to use the intraperitoneal method in the future. Unfortunately, the small batteries proved to be unreliable and most of them failed within four months after the transmitters were implanted (Garshelis and Siniff, 1983).

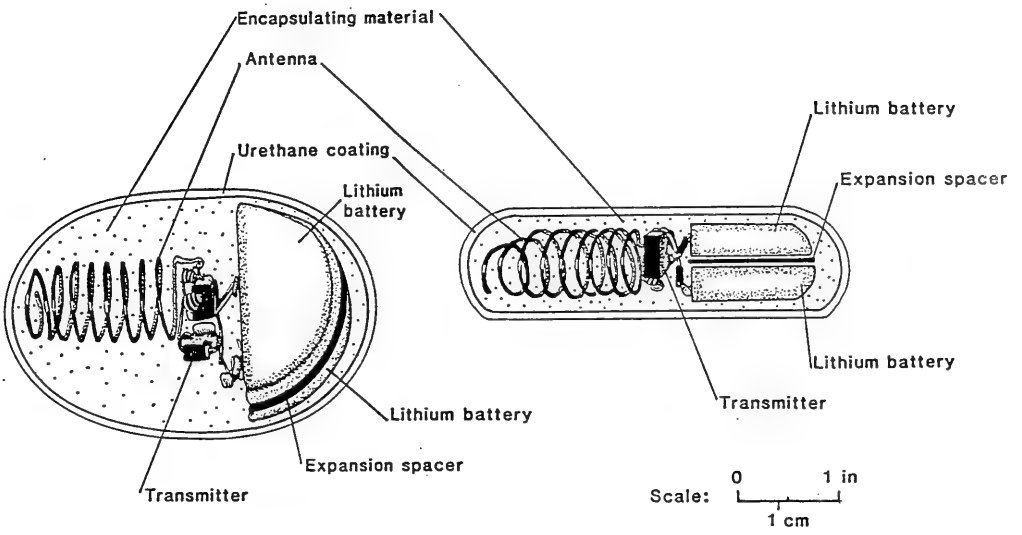
We then designed a new transmitter using lithium batteries developed by the Medtronic Corporation. These batteries were developed for use in medical devices implanted in humans and were known to be extremely reliable in these applications. However, at the request of the U.S. Fish and Wildlife Permit Office, these transmitters were subjected to four months of extensive testing prior to use in California. They were operated under simulated physiological conditions for this entire period, except when undergoing tests at extreme temperature and pressure conditions, and successfully passed all tests.

These transmitters (Figure 1.4) measured about 7.6 x 5 x 2.5 cm and weighed about 120 g in air. This weight ranges from about 1.8 percent (in an 18-lb juvenile) to about 0.4 percent of sea otter body weight (in a 70-lb adult male), thus these transmitters were smaller, relative to body weight, than those used successfully in other species of mammals. For example, Eagle, et al., (1984) used transmitters that ranged up to 3.7 percent of body weight in mink and about 8 percent of body weight in ground squirrels.

They were coated with medical grade Energy Technology Urethane to ensure that they would not produce adverse reactions in biological tissues. They were gas-sterilized and sealed in plastic surgical bags for storage until implanted.

These new transmitters were first used in five animals in California, beginning in March 1984. Their reliability proved to be excellent and their lifespan approached the maximum expected battery life of 700 days. They had a rather limited range of approximately one mile from surface monitoring stations. Engineers at the Cedar Creek Bioelectronics Laboratory then reconfigured the placement of the internal components of the transmitter and redesigned the antenna. These improvements increased the range significantly, up to five miles from surface stations and 10 miles from aircraft. This new design was used in subsequent transmitters, beginning in Alaska in the summer of 1984 and in California in the spring of 1985.

FIGURE 1.4 - A schematic drawing of the implanted radio transmitter used during this study showing its component parts.



Drugs

The otters were immobilized using the methods given in detail in Williams, et al., (1981). Fentanyl was given intramuscularly at dosages of 0.5-0.1 mg/kg of body weight in combination with azaperone at dosages of 0.010 to 0.053 mg/kg. This combination produced a safe, short-acting, and easily reversible immobilizing agent suitable for use under field conditions. The combination of anesthetic and tranquilizer was given to the otters while they were entangled in the gill-net or held in the Wilson trap or dip-net.

Surgical procedures

All surgery in California, and the initial surgery in Alaska, was carried out by Dr. Thomas D. Williams, who developed both the anesthetic procedures (Williams and Kocher, 1978) and the surgical techniques (Williams and Siniff, 1983). In 1984, Dr. Williams trained two other veterinarians to do the operation and they performed some of the operations in Alaska.

Surgery was carried out on a specially constructed operating table, either on board the capture boat or on the beach near the capture site. After an initial health screening procedure, the anesthetized otter was secured to the table with the ventral surface up. The status of the animal was monitored by capillary perfusions, color of the mucous membranes, respiratory rate and depth, temperature, and heart beat. A 50-50 mixture of KY jelly and betadine solution was applied to the ventral midline below the umbilicus and rubbed down to the skin. A comb was used to part the pelage and betadine solution was sprayed over the part. A sterile drape was placed over the ventral abdomen and thorax. Sterile gloves were used for each operation and all instruments were sterilized in benzol.

Tagging

In California, all instrumented animals were tagged on the hind flippers with colored Temple tags. In Alaska, both Temple tags and small button tags were used. The tagging methods and color/location coding system used in California were those used by both the California Department of Fish and Game and the U.S. Fish and Wildlife Service for many years (Ames, et al., 1983). The particular color combination used on each animal was selected in consultation with CDF&G personnel.

Monitoring procedures

We used different monitoring techniques and schedules in California and Alaska because of the climatic and geographical differences between the two areas. It was possible to monitor the animals all year in California but not in Alaska. The usual field season in Alaska extended from late April to mid-September. However, we visited Alaska occasionally during the winter and conducted aerial searches for instrumented animals.

Routine daily monitoring in California was done from the ground. When animals could not be located from the ground, aerial searches were conducted using a small, fixed-wing plane with antennas attached to each wing.

There were no roads in the Alaska study area. Some monitoring was done from a small boat but it was impossible to locate each animal every day due to the large size and complicated geography of the study area. Much of the monitoring was done from the air.

In California, we evaluated the accuracy and precision of the sea otter locations that were obtained by telemetry triangulation. Transmitters were placed in floating buoys and positioned along the coast so that readings could be taken according to the established procedures we used in our monitoring of instrumented otters. The results of this evaluation are presented in Chapter 7.

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CHAPTER 2

REPRODUCTION, SURVIVAL AND TAG LOSS IN CALIFORNIA SEA OTTERS

D. B. SINIFF AND K. RALLS

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INTRODUCTION

The California sea otter population is listed as threatened on the U.S. Endangered Species list and its status and management are of concern to several state and federal agencies. A population model is a basic tool for the understanding and management of any wildlife population. The development of a population model requires reliable estimates of reproductive and survival rates; no estimates of these rates are available for the California sea otter population.

Early knowledge of the general biology of the sea otter reproductive cycle was gained mostly by the examination of reproductive tracts from animals collected in the U.S.S.R. or Alaska (Barabash-Nikiforov, 1947; Sinha, et al., 1966; Kenyon, 1969; Schneider, 1973). These studies showed that the litter size is typically one, with maternal care extending at least four months after parturition, and that a birthing peak occurs in the spring, although birth can occur at any time of year. These early studies generally placed the inter-birth interval at about two years. However, subsequent observations of tagged sea otters in both California and Alaska have indicated that the inter-birth interval is closer to one year (Jameson and Johnson, 1979; Loughlin, et al., 1981; Wendell, et al., 1984). Considerable data on tagged individuals are available for the California sea otter population (Estes and Jameson, 1983; Wendell, et al., 1984) but it has not been possible to obtain good estimates of survival rates from these data for several reasons. For example, information on tag loss rate and difficulty in resighting tagged individuals greatly complicates this estimate. The only available data on tag loss rate is based on the resighting of tagged individuals (Ames, et al., 1983). It is thus an estimate of the rate at which tagged individuals disappear from the pool of regularly re-sighted animals, rather than a direct estimate of the rate at which individual tags are lost.

In this chapter, we present estimates of the proportion of adult females accompanied by pups throughout the year; the inter-birth interval; the period of pup dependency; and reproductive, survival and tag loss rates for the California sea otter population. All estimates are based on observations of telemetry instrumented, flipper-tagged sea otters.

METHODS

We captured 49 otters (Table 2.1). Females known to be pregnant and small pups were not implanted with transmitters. We implanted radio transmitters in 40 otters, which were assigned to age/sex classes on the basis of their weight, estimated age (sometimes from teeth annuli), and, in the

TABLE 2.1 -- Summary of sea otters captured in California during 1984 and 1985.

OTTER NO.	CAPTURE DATE	CAPTURE AREA	SEX	WT. (LBS)	TRANS. FREQ.	LEFT;RIGHT TAG
1	7Mar84	Morro Bay	M	74	723	4/5 red;1/2 silver
2	16Mar84	Morro Bay	M	65	955	4/5 white;1/2 silver
3	21Mar84	Morro Bay	M	44	545	4/5 chartreuse;1/2 silver
4	21Mar84	Morro Bay	M	53	784	4/5 lt. blue;1/2 silver
6+	3Jul84	San Simeon	F	36	807	1/2 orange;1/2 roy.blue
7	15Feb85	Big Sur R.	M	54	333	4/5 pink;4/5 purple
8	1Mar85	Rancho Rico	F#	49	none	1/2 lt. green;1/2 purple
9	1Mar85	Wreck Beach	F	30	233	1/2 silver;1/2 purple
10	1Mar85	Wreck Beach	M	60	041	1/2 lt. blue;4/5 purple
11	15Mar85	Molera Point	F	35	417	4/5 red;1/2 purple
12	16Mar85	Grimes Point	F#	45	none	4/5 chartreuse;1/2 purple
13	16Mar85	Torre Canyon	M	25	461	4/5 white;4/5 purple
14	16Mar85	Torre Canyon	F	41	217	4/5 lt. blue;1/2 purple
15	20Mar85	Torre Canyon	F	43	842	1/2 purple;4/5 orange
16	3Apr85	Wreck Point	F	39	884	4/5 pink; 1/2 purple
17	3Apr85	Grimes Point	M	53	230	1/2 lt. green;4/5 purple
18	3Apr85	Torre Canyon	F#	57	none	1/2 silver;1/2 purple
19	3Apr85	Rancho Rico	F	36	373	4/5 white; 1/2 purple
20	3Apr85	Rancho Rico	F*	16	none	4/5 purple;1/2 purple
21	10Apr85	False Sur	F	45	133	1/2 dk. green; 1/2 purple
22	10Apr85	Big Sur R.	F	42	562	1/2 roy. blue; 1/2 purple
23	10Apr85	False Sur	M	63	062	1/2 roy. blue; 4/5 purple
24	10Apr85	Point Sur	M*	--	none	ear tag 217
--	10Apr85	Point Sur	F	--	none	none
25	13Apr85	Anderson Crk	F	56	933	1/2 orange; 1/2 purple
--	13Apr85	N. of slide	F	--	none	none
--	13Apr85	N. of slide	?*	--	none	none
26	8May85	Little Sur R.	F	46	680	4/5 lt. green; 1/2 purple
27	4Oct85	Dolan Rock	F	46	121	4/5 lt. green; 1/2 purple
28	4Oct85	Esalen	F	36	256	4/5 orange; 1/2 purple
29	11Oct85	Dolan Rock	F	36	655	1/2 silver; 1/2 pink
30	11Oct85	Dolan Rock	M	34	475	1/2 white; 4/5 purple
31	11Oct85	Buck Cr.	F	40	904	4/5 silver; 1/2 purple
32	18Oct85	Buck Cr.	F#	50	none	4/5 gold; 1/2 purple
33	18Oct85	Big Slide	F	46	970	1/2 gold; 1/2 purple
34	19Oct85	J.P. Burns	M	80	625	4/5 lt. blue; 4/5 purple
35	8Nov85	Ragged Pt.	M	35	960	1/2 lt. blue; 4/5 chartreuse
36	8Nov85	County Line	F	37	433	4/5 red; 1/2 chartreuse
37	22Nov85	Beckets Rf.	F	25	380	4/5 orange; 1/2 chartreuse
38	22Nov85	Cypress Ovrl.	F	25	603	4/5 pink; 1/2 chartreuse
39	22Nov85	San Carpoforo	F	30	587	4/5 yellow; 1/2 chartreuse

TABLE 2.1 (continued)

OTTER NO.	CAPTURE DATE	CAPTURE AREA	SEX	WT. (LBS)	TRANS. FREQ.	LEFT;RIGHT TAG
40	17Dec85	Piedras Blan.	F	31	405	4/5 lt. blue; 1/2 chartreuse
41	17Dec85	Piedras Blan.	M	28	152	1/2 orange; 4/5 chartreuse
42	17Dec85	San Carpoforo	F	35	273	4/5 lt. green; 1/2 chartreuse
43	18Dec85	Piedras Blanc	M	31	353	1/2 pink; 4/5 chartreuse
44	18Dec85	Piedras Blanc	F	33	534	4/5 white; 1/2 chartreuse
45	18Dec85	Piedras Blanc	F	27	493	4/5 purple; 1/2 chartreuse
46	18Dec85	San Simeon Pt	F	25	301	4/5 silver; 1/2 chartreuse
47	30Dec85	Lover's Pt.	F	30	028	1/2 pink; 1/2 orange

\+ Otter 5 was captured and tagged by the U.S. Fish and Wildlife Service
\# Pregnant female
* Pup

case of females, reproductive history during the monitoring period. Our sample consisted of nine adult males, five juvenile males, 16 adult females, and 10 juvenile females (Table 2.2).

Adult females were located on an almost daily basis by radiotelemetry. We then attempted to observe them visually through binoculars and a Questar spotting scope (up to 80 power) and record the presence or absence of pups and flipper tags. This was often impossible due to weather conditions, such as fog or rough seas, or difficult lighting conditions. Some individuals were more difficult to observe then others, depending upon their location along the coast. Thus the length of time between visual observations varied across individuals.

To determine the proportion of females accompanied by pups each month of the year, we tallied whether or not each female was accompanied by a pup for every month she was monitored (Appendix 2.1). We considered that a particular female had been accompanied by a pup for a given month if we knew she had been accompanied by a pup for more than a 15 day period that month. If she had been accompanied by a pup for less than a 15 day period, we considered that she had not been accompanied by a pup that month. Months where the status of a particular female was unknown were not counted. The variation in the number of days between sighting of the individual female otters created a problem in calculating the inter-birth interval and the number of days a pup remained with a female. In the case of an inter-birth interval (the time from birth of one pup to birth of the next pup), we usually did not know the exact birth dates of the two pups,

TABLE 2.2 -- A list of sea otters that were instrumented with implanted radio transmitters, their estimated age when available and other vital statistics.

OTTER NUMBER	SEX	WEIGHT (LBS)	ESTIMATED AGE	PUPPED?	AGE/SEX CLASS
1	M	74	--	--	ADULT MALE
2	M	65	--	--	ADULT MALE
3	M	44	--	--	ADULT MALE
4	M	53	--	--	ADULT MALE
6	F	36	--	NO	ADULT FEMALE
7	M	54	7*	--	ADULT MALE
9	F	30	5*	YES	ADULT FEMALE
10	M	60	6*	--	ADULT MALE
11	F	35	--	YES	ADULT FEMALE
13	M	25	--	--	JUVENILE MALE
14	F	41	6*	YES	ADULT FEMALE
15	F	43	5*	YES	ADULT FEMALE
16	F	39	--	YES	ADULT FEMALE
17	M	53	6*	--	ADULT MALE
19	F	36	--	YES	ADULT FEMALE
21	F	45	15*	NO	ADULT FEMALE
22	F	42	8	NO	ADULT FEMALE
23	M	63	5	--	ADULT MALE
25	F	56	7	YES	ADULT FEMALE
26	F	46	--	YES	ADULT FEMALE
27	F	46	10	YES	ADULT FEMALE
28	F	36	13*	NO	ADULT FEMALE
29	F	36	3	NO	JUVENILE FEMALE
30	M	34	2*	--	JUVENILE MALE
31	F	40	11	YES	ADULT FEMALE
33	F	46	10	YES	ADULT FEMALE
34	M	80	8	--	ADULT MALE
35	M	35	2	--	JUVENILE MALE
36	F	37	9	YES	ADULT FEMALE
37	F	25	2	NO	JUVENILE FEMALE
38	F	25	1*	NO	JUVENILE FEMALE
39	F	30	2	NO	JUVENILE FEMALE
40	F	31	3	NO	JUVENILE FEMALE
41	M	28	2	--	JUVENILE MALE
42	F	35	2	NO	JUVENILE FEMALE
43	M	31	<1	--	JUVENILE MALE
44	F	33	2	NO	JUVENILE FEMALE
45	F	27	1	NO	JUVENILE FEMALE
46	F	25	2	NO	JUVENILE FEMALE
47	F	30	<1	NO	JUVENILE FEMALE

*The teeth from these individuals were damaged so that only a minimum age could be estimated.

although we knew that each birth occurred within some time period. For example, if we saw an instrumented female without a pup on 1 April and saw her again with a pup on 10 April, the pup had obviously been born between these two dates. Suppose we continued to monitor this female throughout the period of pup dependency and her next pregnancy. We last saw her without a pup on 15 March of the following year but she had a pup when next seen on 10 April. There were thus two intervals when her reproductive status was unknown. The first interval was 10 days and the second was 26 days. To calculate the inter-birth interval, we added one-half of each of these intervals to the number of days between the first sighting of the female with a pup one year and the first sighting of this female with her next pup. For our example, then, the inter-birth interval was 383 days -- 365 days from 10 April of the first year to 10 April of the second year plus five days from the interval between 1 April and 10 April spanning the birth of the first pup and 13 days from the interval between 15 March and 10 April spanning the birth of the subsequent pup. To make this calculation, we arbitrarily included for the interbirth interval estimates, only data for which neither of the unknown status intervals was more than 51 days.

The same problem arose in calculating the number of days the pup remained with the female. Again, there were two intervals when the status of the pup was unknown, one spanning its birth and a second spanning its disappearance. As before, we used only data in which both intervals for which the status of the pup was unknown were less than 52 days. We divided each interval in half and added it to the period between the first and last dates the pup was seen with the female.

We estimated the annual reproductive rate in two ways. The first method was based on the total number of days all the adult females were monitored and the known number of pups born to them during this period. This calculation again included intervals when the adult females were not seen and their status was unknown. The longest such intervals were 10 months for one female (otter 11) and four months for another (otter 16) (Appendix 2.1). We summed the total number of monitoring days across 13 adult females, and divided this figure by the total number of pups produced to obtain the average number of days required to produce a pup. This average number of days was then divided into 365 to obtain an estimate of the annual pupping rate.

In the second method, we considered only the five females used to calculate the inter-birth interval and the period the pup remained with the female. For this data set, we divided the average inter-birth interval into 365 to obtain an estimate of the annual pupping rate.

Our first method of estimating the annual reproductive rate is probably most similar to that which one would use for tag-resight data (Wendell, et al., 1984), where females are observed periodically and their reproductive status noted. This method also produces gaps where the status of the female is unknown; the length of these gaps varies with the frequency of the attempts to re-sight the females and the difficulty of observing each female.

The estimation of survival rates from radiotelemetry data may be approached somewhat differently than that from data derived from resighting or recapture of tagged animals. Instrumented animals are known to be alive or dead on a daily basis. Thus the procedure that has been developed for radiotelemetry data is to estimate a daily survival rate and expand it to the time period desired, usually one year, assuming that the daily rate remains constant over this period (Heisey and Fuller, 1985). The formulation recommended by Heisey and Fuller is:

$$\text{Annual Survival} = \frac{(\text{Transmitter days} - \text{deaths})^{365}}{\text{Transmitter days}}$$

When days are used as the basic time interval, it is necessary to assume that the status of each individual (dead or alive) is known for each day. This assumption was not fulfilled for our animals when individuals disappeared and we were unable to determine their fate. These individuals were classified as missing (Appendix 2.2), and these individuals might have died or their transmitters might have expired. Animals classified as transmitter failed, transmitter expired, or transmitting were known to be alive at the number of days indicated in Appendix 2.1. The way in which these missing animals are treated can affect the survival rate estimate. One way to handle this problem is to assume that transmitters are extremely reliable for some number of days, and animals lost prior to this time have died. We used 450 days for this decision point for missing animals. Thus, we assumed that otters missing in less than 450 days from the capture date had died and that those missing after 450 days were alive on the date they became missing. This criterion was based on the average life span, 485 days, of the five transmitters in which expiration was verified. We also calculated survival rates for each age/sex class by using the number of individuals in each sex and age class as the basis of calculations. This means following the binomial model:

$S = 1 - {}^{D}/n$ where:

S = Estimate of survival
D = number of animals that died
n = sample size for the particular sex/age category.

For this model an estimate of variance is easily calculated by the standard:

$$s^2 = {}^{pq}/_{n} \quad \text{where:}$$

p = survival rate estimate
q = D/n, or the proportion dying

It only remains to specify the time interval, which is normally taken to be one year. However, in this case we followed the same 450 day criterion. Thus the binomial model for an estimate of the annual survival rate becomes:

$$S = (1 - {}^{D}/_{n})^{365/450}$$

We estimated annual survival rate each of these ways for the four sex and age classes of adult females, adult males, juvenile females and juvenile males.

The pup survival rate was based on the ratio of the number of pups that died during the period of dependency to the number of pups born, over the entire monitoring period. We assumed that pups that remained with the female less than 150 days died, based on an estimated pup dependency period of six months (Payne and Jameson, 1984; Wendell, et al., 1984).

One of the advantages of being able to locate animals by radiotelemetry is that they are still identifiable after tag loss has occurred. All of our instrumented animals were tagged with one Temple tag in each hind flipper, following a procedure developed by the California Department of Fish and Game (Ames, et al., 1983). In addition, the tags were drilled so that a small nylon or stainless steel screw could be used to hold the two sides of the tag together. A small amount of glue was dripped into the hole before the screw was inserted. Our data on the presence or absence of tags were similar to our data on reproduction. However, tags were more difficult to see than pups, so many of the intervals between the last date a tag was seen and the first date it was seen to be missing were longer than the corresponding intervals for pups. We analyzed these data using the same method we used to analyze the data on the survival of individual otters. However, we assumed that a tag had survived until the date it was seen to be missing and thus calculated only the maximum possible tag survival rate.

RESULTS

Although some proportion of adult females were accompanied by pups throughout the year, this proportion peaked in the spring, with a secondary peak in the fall (Fig.2.1). Our total reproductive data set includes information on the 13 adult females that were monitored at least 355 days (Table 2.3). However, our best data for the determination of the inter-birth interval and the period the pup remained with its mother came from five females for which the length of all three intervals in which their status was unknown (those spanning the birth of the first pup, the disappearance of the

Table 2.3 -- Reproductive and age data and length of monitoring period for adult female sea otters.

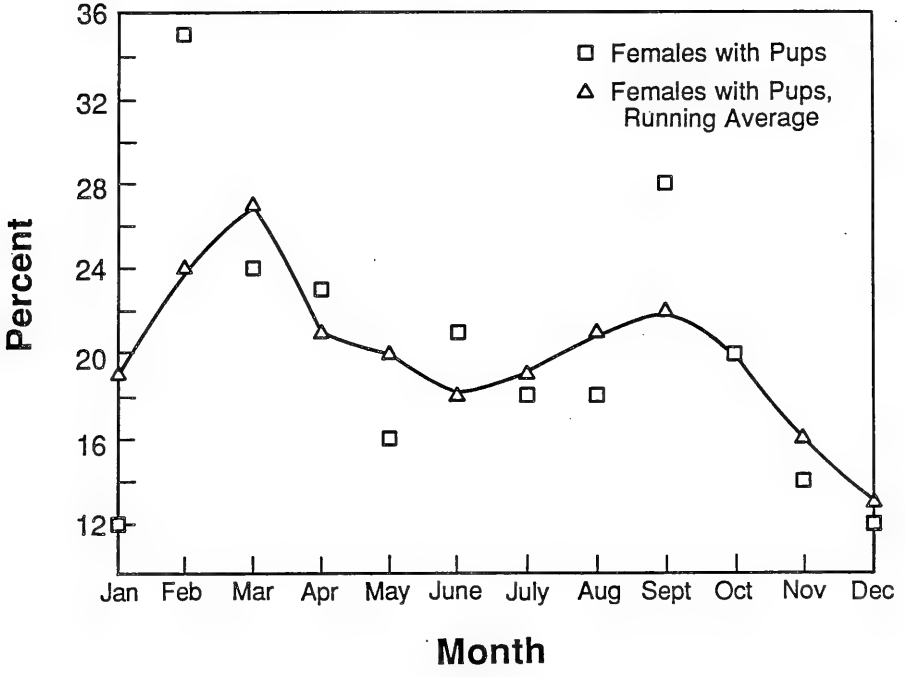
OTTER NUMBER	AGE (YRS)	DAYS MONITORED	PUPS BORN	PUPS DIED
6	-	355	0	0
9	5*	544	2	1
11	-	621	1	0
14	6*	744	2	0
15	5*	725	1	0
16	-	608	2	0
19	-	587	3	0
22	8	585	0	0
25	7	555	1	0
27	10	540	1	1
31	11	637	2	2
33	10	630	2	2
36	9	609	2	2
TOTALS		7740	19	8

*Only a minimum age could be estimated from these individuals due to tooth damage.

first pup, and the birth of second pup) was less than 52 days (Table 2.4). For this data set, the average inter-birth interval was 416 days. Our first estimate of the annual reproductive rate is based on the information summarized in Table 2.3. Nineteen pups were produced during 7,740 monitoring days; thus, an average of 407 days was required to produce one pup, and the estimated annual reproductive rate is 0.90 pups per adult female. Our second estimate is based on the data in Table 2.4. The average inter-birth interval is 416 days, which corresponds to an annual reproductive rate of 0.88 pups per adult female per year.

Eight of the 19 pups almost certainly died before

FIGURE 2.1 - The percent of the adult female study animals in California that were with pups during each month of the year.



weaning, giving an estimated pup survival rate of 0.57 (Table 2.5). We estimated that these eight pups (Table 2.4B) remained with their mother for less than 65 days. Our estimate assumes that pups born shortly before the females' transmitters expired lived, when in fact we were unable to determine their fate, and it may exclude some pups that lived only a short time and were thus undetected (Appendix 2.1).

Considering all 80 flipper tags in our sample (Appendix 2.3), the estimated annual tag survival rate was 0.74 (Table 2.6A). Survival rates for right and left tags were not significantly different. However, more otters lost two tags than would be expected by chance, based on the assumption that tag loss follows a binomial distribution. Using the number of tags lost over the period of monitoring to derive the expected probabilities of losing one, two, or no tags and comparing these expected values to the data, we see that significantly more otters lost both tags than expected (Table 2.6C). This result is perhaps not surprising, as some individuals have been seen to bite and manipulate their flipper tags, ultimately removing them, while other individuals appear to ignore the presence of tags. If the otters that lost two tags are excluded, the estimated annual tag survival rate increases to 0.91 (Table 2.6B).

Both methods for estimating survival rates for the four main age/sex classes, indicated the highest survival for adult females and lowest for adult males (Table 2.5). Estimates for juvenile females were lower than those for adult females, while estimates for juvenile males were higher than those for adult males. The survival rate of juvenile females was lower than that of juvenile males for both methods of estimation. The data on which we based these estimates are presented in Appendix 2.2.

DISCUSSION

Our data on the proportion of females accompanied by pups over the yearly cycle, which show a peak in the spring and a smaller peak in the fall, are similar to data on the proportion of pups to independent otters recorded by the California Department of Fish and Game in their monthly counts of index areas (Brody, Chapter 10). The independent otters in these index areas are probably largely adult females along with a few territorial males and juvenile females. This bimodal pattern could be the result of females that successfully raise pups having a longer inter-birth interval than those that do not, thus placing the birth of their next pup at one year plus three to four months. Our data are in agreement with the emerging consensus that many female sea otters pup on an approximately annual basis (Loughlin, et al.,

Table 2.4 -- Reproductive information on adult female sea otters that were known to have given birth to at least one pup. The table gives the number of days during which the reproductive status of these females was known and unknown (A). Calculated periods with and without pups and inter-birth intervals for those animals where the unknown intervals were not more than 51 days are shown below (B).

A. DATA

Otter	Unknown Status (Days)	Known Days With Pup One	Unknown Status (Days)	Known Days Without Pup	Unknown Status (Days)	Known Days With Pup Two	Unknown Status (Days)
9	13	36	11	330	51		
11	113	1	318				
14	11	149	20	390			
15	2	81**					
16	41	117	104	101	120	28**	
19	68	85	80	91	57	39	5
25	2	176	8				
27	11	24	26				
31	8	16	8	313	28	41	20
33	10	31	2	376	5	8	19
36	37	26	2	258	17	1	5

B. CALCULATED VALUES

OTTER NUMBER	PERIOD WITH PUP (DAYS)	PERIOD UNTIL NEXT BIRTH (DAYS)	INTER-BIRTH INTERVAL (DAYS)
9*	48	361	409
14*	165	421	586
25	181		
27	43		
31*	24, 65	331	355
33*	37, 20	380	417
36*	46, 12	266	312
	MEAN = 64	MEAN = 416	

* Five females used to calculate the inter-birth interval.
** Still with pup when last seen.

Table 2.5 -- Annual survival rate estimates. Two estimates were made for the age/sex categories of adult females, adult males, juvenile females and juvenile males. The first was obtained by converting the daily survival rate of radio-instrumented otters to an annual rate (Heisey and Fuller, 1985). The second used the standard binomial model (see text for explanation) and the status of individual sea otters as a basis for the estimate. The estimated pup survival rate was based on the pups born to the instrumented females.

	TRANSMITTER DAYS AS THE BASIS*	INDIVIDUALS AS THE BASIS*	
	SURVIVAL	SURVIVAL	STANDARD DEVIATION
ADULT FEMALES	0.91	0.89	0.088
ADULT MALES	0.61	0.52	0.167
JUVENILE FEMALES	0.80	0.75	0.145
JUVENILE MALES	0.88	0.85	0.179

*Animals that were classified as missing before 450 days were assumed to have died at the time they became missing, while those classified as missing after this time were assumed to have been alive when they became missing.

PUPS TO WEANING 0.57

1981; Estes and Jameson, 1983; Wendell, et al., 1984; Garshelis, Johnson, and Garshelis, 1984). Our average inter-birth interval of 416 days is clearly within the range of the 17 intervals recorded by Wendell, et al., (1984) based on observations of tagged otters. Although our sample size is smaller than theirs, the intervals when the reproductive status of the female was unknown tended to be smaller in our data. One interesting aspect of our data is the rather large degree of variation, with a range of 312 to 611 days. The reason for this variation may be correlated with the length of the dependency period. It is generally agreed that female otters rarely, if ever, mate when accompanied by a pup (Kenyon, 1969; Calkins and Lent, 1975; Garshelis, et al., 1984). Clearly more data are needed on the relationship between the inter-birth interval and the period of pup dependency, which probably varies with the age and condition of the female.

Minimum reproductive rates for sea otters in Alaska have been suggested by the reproductive condition of females in samples killed in late winter and spring (Kenyon, 1969; Schneider, 1973). Kenyon (1969) found that 71% of animals collected in this period were pregnant and 17% had recently

Table 2.6 -- Estimates of annual tag survival rates based upon the survival rate estimation procedures for instrumented animals as outlined by Heisey and Fuller (1985). The only difference here is that the "death" of tags rather than individuals is the unit of measure (A and B). A comparison of tag loss to expected tag loss based on the binomial distribution is shown in C.

A. ALL OTTERS

TAG	ANNUAL SURVIVAL RATE	NUMBER OF TAGS LOST (OF 80)
RIGHT	0.70	13
LEFT	0.78	10
ALL	0.74	23

B. EXCLUDING OTTERS THAT LOST TWO TAGS

TAG	ANNUAL SURVIVAL RATE	NUMBER OF TAGS LOST (OF 64)
ALL	0.91	6

C. COMPARISON OF TAG LOSS TO THE BINOMIAL DISTRIBUTION
ESTIMATED PROBABILITY OF LOSING ONE TAG = 23/80 = 0.2875

NUMBER OF TAGS LOST	NUMBER OF OTTERS	EXPECTED FROM BINOMIAL MODEL
NONE	25	21
ONE	8	16
TWO	7	3

$P<0.05$, CHI-SQUARE = 61, 1 D.F.

given birth. Schneider (1973) found that for samples collected in May, 59% were pregnant and 14% had recently given birth. Combining these values gives approximate annual rates of .88 and .73 for these two studies, respectively. No estimates are available for the California population. Our estimates, based on the number of pups born during the monitoring period and the average inter-birth interval are, as expected, slightly higher than the minimum rates available

for Alaska since ours include the complete annual cycle. Because of the sea otter's ability to produce pups throughout the year, and the probable relationship between the inter-birth interval and the period of pup dependency, it seems likely that estimates of annual reproductive rates in sea otters will be quite dependent upon conditions during the particular interval during which the data are collected.

Our estimated survival rate for pups from birth to weaning, 0.57, while possessing the potential for bias, as mentioned under results, is close to the 0.50 estimate needed

TABLE 2.7 --A comparison of the age of pups at separation from the female in California and Alaska, based on our data and other published data.

DAYS PUP WITH FEMALE	ALASKA*	CALIFORNIA**
0-50	0	8
51-100	3	3
101-150	1	2
151-200	4	5

* Data from Garshelis (1983).
** Data from Table 2 plus eight pups from Loughlin, et al., (1981).

to produce a zero population growth rate in our population model when combined with our other survival rate estimates (Chapter 10). Surveys suggest that the population has been stable over the past decade (Estes and Jameson, 1983). Table 2.7 contrasts survival patterns of dependent pups in California and Alaska. Early mortality appears to be more frequent in California. This pattern, if confirmed by additional data, may be a result of storm patterns in California, because the Alaskan data were collected in Prince William Sound, which provides more shelter during periods of inclement weather.

The annual survival rate estimates we obtained by expanding the daily survival rate based on transmitter-days also appear reasonable. The relatively close correspondence between the estimates calculated by two different methods is encouraging, as is their general agreement with other aspects of the data collected on our instrumented animals, such as the

movement patterns, time budgets, and feeding patterns of the different age/sex groups.

Our adult females, which had the highest survival rates, were in areas of the range where human activities were minimal and they traveled the least of the four sex/age groups. Adult males had lower survival rates than adult females and juveniles of both sexes. A low survival rate for adult males is also suggested by the sex ratios in the California Department of Fish and Game database on dead sea otters. Considering only the carcasses in good condition, where the sex of the carcass was known in almost all cases, significantly more dead adult males than adult females washed ashore (Table 2.8). Our adult males tended to be particularly vulnerable during periods of travel. One was shot after he had moved a considerable distance from his capture location and two others disappeared when they were moving through areas in which gill-net boats were operating. Juvenile males also traveled extensively but tended to remain farther offshore, which may provide some degree of protection from human activities, such as shooting (Wild and Ames, 1974; Morejohn, et al., 1975) and incidental capture in gill-nets (Wendell, et al., 1986), and contribute to their higher survival rate. The only juvenile male that died during our study was almost certainly attacked by a shark.

Table 2.8. - The California Department of Fish and Game maintains a data-base on the dead sea otters that wash ashore. Each carcass is given a condition rating, aged and sexed if possible. Numbers of male and female carcasses in good condition are compared to those expected if the sex ratio was equal.

AGE CLASS (after Morejohn et al. 1975)	SEX				
	MALES		FEMALES		
	Observed	Expected	Obs.	Expected	
Pups/immatures	52	53	54	53	ns
Subadults	23	21.5	20	21.5	ns
Adults	84	69.5	55	69.5	$p<0.05$*
Old adults	29	28	27	28	ns

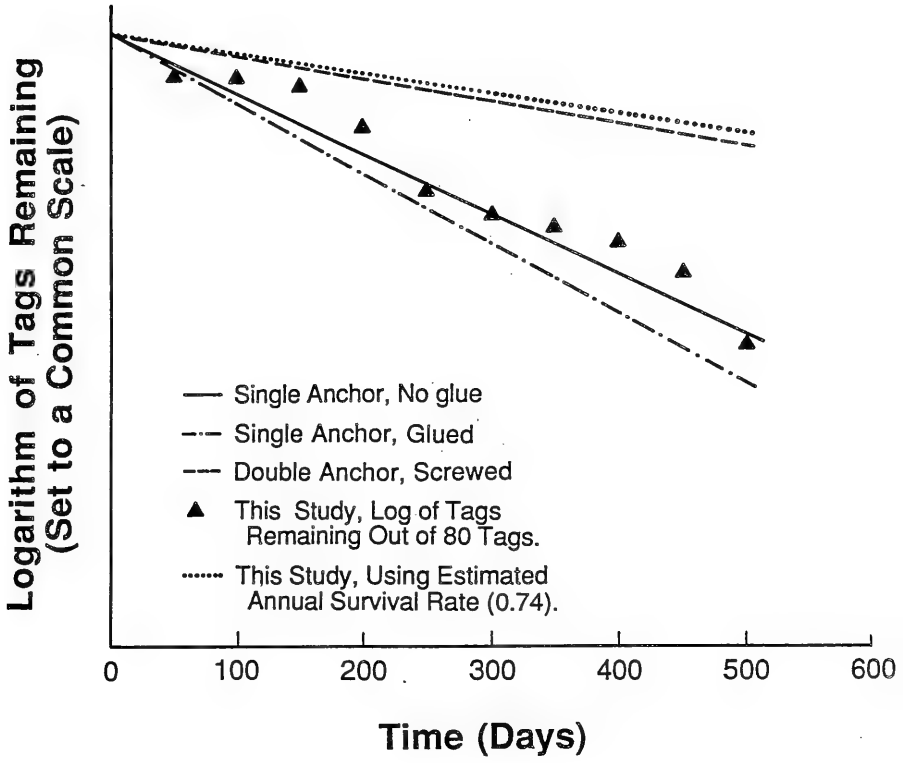
*Chi-square = 6.1, 1 d.f.

Juvenile females had low survival rates compared to adult females. They also had slightly lower survival rates than juvenile males, as did the juvenile females in Alaska (Chapter 9). However, in the CDF&G database on dead sea otters, again considering only the carcasses in good condition, the number of juvenile male and female carcasses was about equal, suggesting similar mortality rates for the two sexes of juveniles in California. Juvenile females in California clearly foraged longer than other otters to obtain sufficient food (Chapters 4 and 5) and one juvenile female in Alaska starved to death (Chapter 9). Taken as a whole, our data strongly suggest that the age/sex groups are differentially affected by the various sources of sea otter mortality.

Our observations of tags on instrumented individuals provide estimates of annual tag loss rates that exclude the possibilities that mortality and movements of tagged individuals out of the study area added to the perceived tag loss. The annual tag survival rate of 0.74 represents a good estimate for the Temple tag. The only other estimates of tag loss rates are those of Ames, et al., 1983, who used three methods of tag application and used resightings of individuals over time to estimate loss rate. The use of resighting information to estimate tag loss has the potential to include loss due to death and movement of individuals out of the study area in addition to tag loss, and thus one would expect it to overestimate actual tag loss. Curiously, however, using our annual tag survival of 0.74 (which excludes the other sources of loss of mortality and movement of the area), we found the loss rate to correspond almost exactly to the loss rate for double-anchored tags in Ames, et al., 1983 (Fig. 2.2). When we used our data and plotted the number of tags remaining on the otters that were still being located on a regular basis against time (subtracting from the original 80 tags all those that were on otters with failed or expired transmitters and on missing and dead otters plus those that were lost by animals with functioning transmitters), the estimated tag loss was of course higher and corresponded very closely to that for the other two methods of tag application (single anchor, unglued; and single anchor, glued) in Ames, et al., 1983 (Fig. 2.2).

Ames, et al., found that the apparent loss rate of double-anchored tags was less than the apparent loss rate of single-anchored tags (whether glued an unglued). Our data suggest two possible reasons for this difference. The first possibility is that the retention of double-anchored tags was very high and the observed loss rate was almost entirely due to mortality and/or movements out of the study area. The second is that the small number of animals on which this method was used rarely, if ever, moved out of the study area and did not suffer significant mortality during the study

FIGURE 2.2 - A comparison of tag-loss rates between this study and the study of Ames, et al, 1983. (See text for explanation.)



period. These conditions could occur, for example, if the tagged individuals were mostly adult females.

Considerable data can be obtained by following tagged animals and tag-resight data can potentially be used to estimate annual survival rates for the various age/sex classes of a species. However, mark-recapture techniques, using the appropriate models, must be used for these survival rate estimates (Seber, 1973). For sea otter tag-resight data, the combined effects of unequal probability of sighting among individuals, movement of animals out of the intensive study area, and differential mortality patterns among age/sex groups make the application of such methods extremely difficult. When tag loss is added to these complications it becomes rather unlikely that accurate estimates of annual survival rates for sea otters can be derived from such data. Furthermore, the comparison of our data with those of Ames, et al., (1983) suggests that for sea otters, even under the best conditions, it would be difficult to separate tag loss from actual mortality and movement away from the study area. In our study, known tag loss, added to verified mortality, would have produced unrealistically low survival rate estimates.

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CHAPTER 3

MOVEMENT PATTERNS AND SPATIAL USE OF CALIFORNIA SEA OTTERS

K. RALLS, T. EAGLE, AND D. B. SINIFF

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INTRODUCTION

Sea otters tend to be sexually segregated in "male areas", occupied largely by males, and "female areas", inhabited by adult females and their young (Kenyon, 1969; Schneider, 1978). Breeding males maintain territories, either seasonally (Garshelis and Garshelis, 1984) or all year (Loughlin, 1980), within the "female areas". Male territories are often smaller than the home ranges of adult females (Loughlin, 1980; Garshelis and Garshelis, 1984), although life-time home ranges of males may exceed those of females (Kenyon, 1969; Garshelis and Garshelis, 1984).

In Alaska, home ranges consist of extensively used areas connected by travel corridors (Garshelis and Garshelis, 1984; Chapter 8). Long-distance seasonal movements between "male areas" and "female areas" have been documented in both Alaska and California: four adult males moved over 100 km in Alaska (Garshelis and Garshelis, 1984) and three males moved over 80 km in California (Ribic, 1982). Movement patterns of juvenile sea otters in Alaska have been studied by Monnett and Rotterman (Chapter 8); few data are available on the movement patterns of juveniles in California.

Sea otters are a coastal species, although they may be found quite far from shore in shallow-water areas (Kenyon, 1969). Loughlin (1980) and Ribic (1982) reported that they rarely venture beyond the outer limits of the kelp canopy in California.

We report here on the movement patterns and spatial use of 38 California sea otters representing all four major age and sex classes: adult females, adult males, juvenile females, and juvenile males. The otters were instrumented with implanted radio transmitters. Because these transmitters had a much longer life span than those used in previous studies and we attempted to locate each individual every day, our data provide a more detailed picture of sea otter movement patterns and spatial use than previously available.

METHODS

Otters were assigned to sex and age classes based on their weight at capture, estimated age based on the examination of cementum layers in the vestigial premolar extracted for this purpose, and, in the case of females, reproductive performance. All juveniles were judged to be no more than two years of age (Chapter 2).

We usually attempted to locate each instrumented otter on a daily basis by listening for their radio signals from points along the shore. Individual otters were located at

various times of day, depending upon their movements from the previous day and our searching pattern. Sometimes, usually when an animal had moved a considerable distance from its previous location, an individual could not be located for several days. We searched for missing individuals from the air; this was generally successful, as the radio signal could be heard from a greater distance from the air than from the shore. Location data were also recorded once an hour during 24-hour watches.

Three methods were used to estimate the position of a otter once its radio signal was detected: visual observation of the otter, triangulation on the radio signal, and, when neither of these was possible, the best judgement of the researcher based on the direction and strength of the radio signal. The accuracy of the locations determined by triangulation was estimated by triangulating on radio signals from transmitters attached to buoys at known locations (Chapter 7). The method by which each location was estimated was coded in the data, enabling us to analyze only those locations determined by a particular method when appropriate. Unless otherwise noted, all location data were included in an analysis. Triangulations were plotted on topographic maps of the study area; locations were recorded in the form of x-y coordinates based on the UTM grid.

We used several measures in our analyses. The average distance between successive locations of each individual otter, separated into those recorded between 18 and 36 hours apart and those recorded more than 36 hours apart, was used to compare the usual distance traveled on a short-term basis among the age/sex classes. This distance was measured on the UTM grid and is the straight line distance between the two locations. The path taken by the otter was probably longer.

The area used by individual otters on a daily basis was calculated from the hourly triangulated locations recorded during 24-hour watches, using the minimum convex polygon method commonly used for terrestrial mammals (Hayne, 1949).

To portray the movement patterns of individuals over the entire monitoring period, we moved each daily location for an individual to the nearest point along the 5-fathom contour. We then calculated the deviation of each daily location from the mean location for that otter along this contour and plotted these daily deviations against time.

Only daily locations determined by triangulation were used to estimate distance offshore. The coastline was digitized in UTM coordinates and a BASIC program was written to calculate the distance from each otter-location to the nearest point on the shore.

Monthly movement patterns were examined using the average general harmonic mean distance (Hp) (Neft, 1966). This measure, which is calculated from the distance between all of an otter's locations for a given month, is insensitive to a few long distance movements, and thus, may better reflect Burt's (1943) conception of the home range. At least seven locations in a month were required before Hp was calculated.

The "distance between extreme locations" (DBEL) was used to compare the length of coastline frequented by individuals over the entire monitoring period. This measure was first used by Garshelis and Garshelis (1984) in their studies of sea otters in Prince William Sound, Alaska, and is the distance between the two farthest-apart locations of an individual otter over the period of time it was monitored. It can be considered an approximation of an otter's range during the monitoring period. It is particularly useful for comparisons between California and Alaska data, as field conditions in Alaska preclude collection of the daily locations of each otter that enabled us to calculate other measures for the California otters. This distance was measured on the UTM grid.

Statistical comparisons among age and sex classes were performed using analysis of variance, controlling for variation among individuals within classes. We performed a log (base 2) transform on the data to reduce heterogeneity of variances. All statements that differences are statistically significant are based on the 0.05 probability level.

RESULTS

Distance between successive locations

Otters of all age and sex classes were usually found within a comparatively short distance of their location on the previous day. Data on the distance between successive locations were divided into two categories: those recorded within 18-36 hours of the previous location of that individual and those recorded after an interval of more than 36 hours (Tables 3.1 and 3.2). Analysis of variance (Appendix 3.1) indicated that significant variation occurred among individuals within all the age and sex classes in both categories except for the juvenile males in the greater than 36 hour category. This suggested that individual movement patterns from one day to the next were different for young males but that their long term patterns were similar. However, juvenile males were the most similar in both the 18-36 and more than 36 hour categories. The variation among the sex/age classes was much greater than that within classes. For all these data, even though a log transformation was used

to improve the homogeneity of the within individuals "variance", Bartletts test for homogeneity showed significant differences in all cases.

TABLE 3.1 - Average distance (km) between successive locations, recorded between 18 and 36 hours apart, for each instrumented otter along the California coast. AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

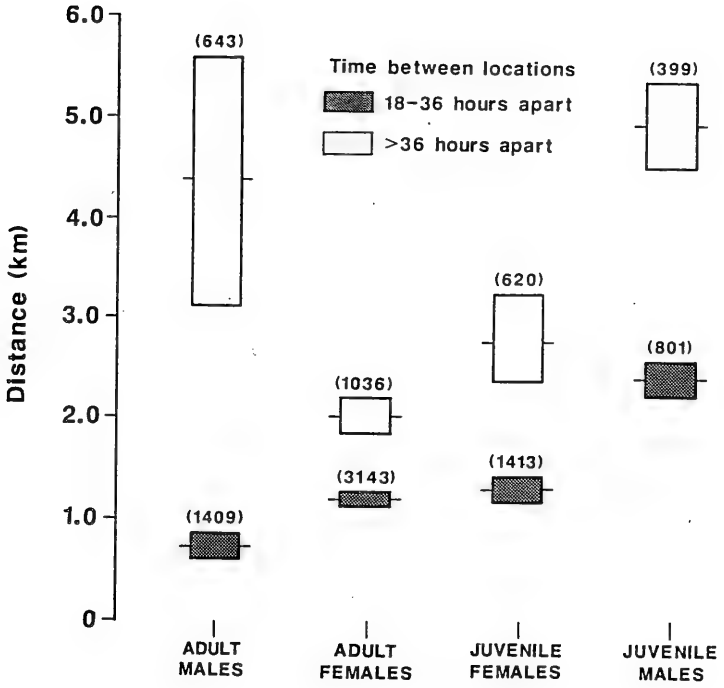
OTTER NUMBER	AGE/ SEX	MEAN	N	STANDARD DEVIATION
15	AF	0.355	342	0.428
28	AF	0.434	10	0.124
4	AM	0.489	115	1.004
7	AM	0.517	326	0.485
10	AM	0.711	282	1.661
1	AM	0.717	229	4.119
2	AM	0.724	89	1.939
33	AF	0.757	272	1.056
17	AM	0.773	138	1.147
46	JF	0.823	375	0.731
42	JF	0.825	345	1.806
11	AF	0.897	311	0.806
19	AF	0.900	194	1.493
16	AF	0.909	248	1.396
36	AF	0.918	390	0.855
9	AF	1.018	265	1.113
3	AM	1.044	183	3.152
6	AF	1.091	101	1.522
25	AF	1.105	284	1.629
38	JF	1.134	18	0.928
45	JM	1.244	164	1.836
37	JF	1.260	117	1.677
40	JF	1.284	285	3.206
31	AF	1.369	308	1.463
27	AF	1.453	180	1.692
47	JF	1.536	66	1.378
39	JF	1.680	244	3.187
44	JF	1.716	77	3.314
34	AM	2.051	47	5.946
29	JF	2.165	237	2.547
43	JM	2.170	186	2.159
41	JM	2.299	229	2.335
22	AF	2.354	187	2.944
26	AF	2.401	12	1.796
14	AF	2.409	381	3.282
13	JM	2.569	83	5.488
35	JM	2.744	241	4.821
30	JM	2.961	230	3.339

TABLE 3.2 - Average distance (km) between successive locations, recorded more than 36 hours apart, for each instrumented otter along the California coast. AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

OTTER NUMBER	AGE/ SEX	MEAN	N	STANDARD DEVIATION
15	AF	0.417	108	0.462
28	AF	0.912	6	1.155
33	AF	0.998	149	1.364
46	JF	1.077	119	1.115
44	JF	1.120	36	0.971
36	AF	1.177	105	0.977
42	JF	1.302	107	2.301
11	AF	1.388	104	1.301
31	AF	1.393	121	1.411
7	AM	1.405	101	5.453
38	JF	1.407	10	1.323
9	AF	1.496	97	2.080
25	AF	1.579	96	2.465
1	AM	1.587	70	7.452
37	JF	1.608	70	2.389
19	AF	1.646	136	2.398
2	AM	1.652	31	3.181
10	AM	1.773	125	8.601
47	JF	1.936	178	1.928
16	AF	1.973	123	3.325
6	AF	2.017	66	1.903
26	AF	2.126	7	1.191
27	AF	2.336	92	2.428
4	AM	2.343	115	9.117
3	AM	2.442	94	7.626
45	JM	2.514	102	4.740
29	JF	3.346	110	3.980
41	JM	3.499	82	3.726
14	AF	3.546	133	4.533
17	AM	4.524	52	10.050
40	JF	4.562	115	14.330
22	AF	5.137	124	6.954
35	JM	5.295	84	9.836
43	JM	5.424	129	9.360
13	JM	6.220	136	12.030
39	JF	6.552	76	11.470
30	JM	8.075	118	15.740
34	AM	28.070	55	46.420

To illustrate the relatively short-term movement patterns of the four age/sex classes, we plotted the average movement between successive locations for all eight data sets, e.g.

FIGURE 3.1 - A comparison of the average distance between successive locations for the age/sex categories of adult females, adult males, juvenile females, and juvenile males, calculated for locations made 18-36 hours apart and those made after more than 36 hours.



adult males, adult females, juvenile females and juvenile males for both the 18-36 hour data set and the >36 hour data set, plus or minus two standard errors of the mean (Fig. 3.1). Within the 18-36 hour data set, the distance moved between successive locations was relatively consistent, averaging around 1 km, the exception being the juvenile males, who averaged about 2.3 km, significantly greater than the other age/sex classes. Adult males showed much more variation in the >36 hour data set than in the 18-36 hour data set. This variation reflects the occasional long-distance movements of adult males, which often resulted in the animals not being located for several days. Juvenile males and juvenile females also made these long-distance movements but there was more consistency within these classes with respect to the distance traveled on such trips.

In general, otters tended to stay within a small area for an extended period and then suddenly move for a considerable distance. Tables 3.1 and 3.2 do not illustrate the distance which an individual otter can travel from one day to the next during these periods of rapid movement. To give a sense of this distance, we plotted the 20 longest movements (again using the UTM grid) made within 18 to 36 hours for otters belonging to each age/sex class (Fig. 3.2). The longest daily movements were 47.5 km for an adult male, 40.1 km for a juvenile female, 38.8 km for a juvenile male, and 17.5 km for an adult female. However, movements of more than 10 km a day were infrequent.

Daily convex polygon areas

Areas used by individual otters over a 24-hour period ranged from 10 to over 1000 ha (Table 3.3). Adult males were not included in the analysis of variance (Appendix 3.2) because of insufficient sample size. For the other three age/sex classes, there was no significant variation within age/sex classes but variation among classes was significant. Juvenile males tended to travel over a larger area than individuals of the other age/sex classes.

Long-term movement patterns along the coast

The average location along the California coast for each instrumented otter is shown in Fig. 3.3. Figures 3.4, 3.5, 3.6, and 3.7 illustrate both the substantial degree of variation between individuals within age/sex classes in the extent to which they travel away from this average location and the way in which many otters tend to remain within small areas for extended periods of time and then suddenly move a much greater distance.

FIGURE 3.2 - A plot of the 20 longest trips made between successive locations that were 18-36 hours apart for the four age/sex categories of adult females, adult males, juvenile females, and juvenile males.

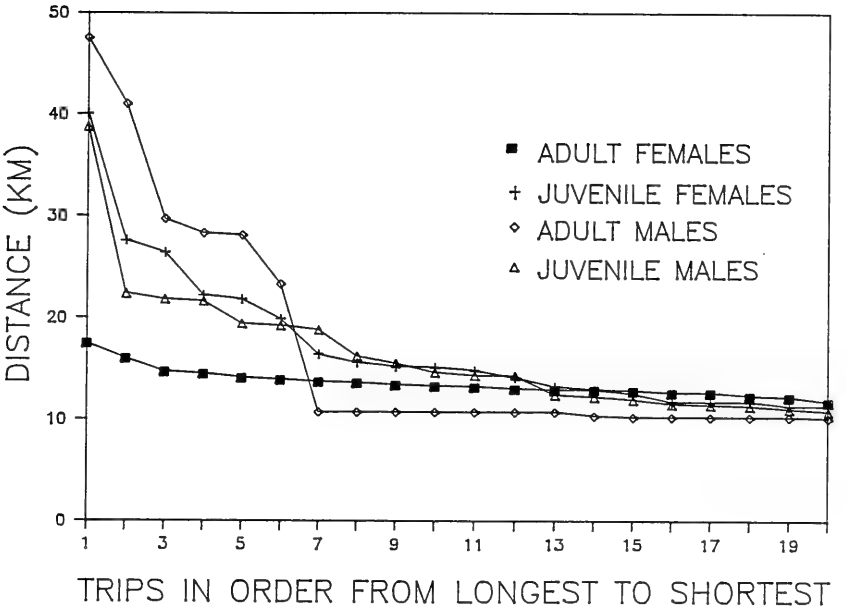


FIGURE 3.3 - The average locations of the instrumented sea otters along the California coast.

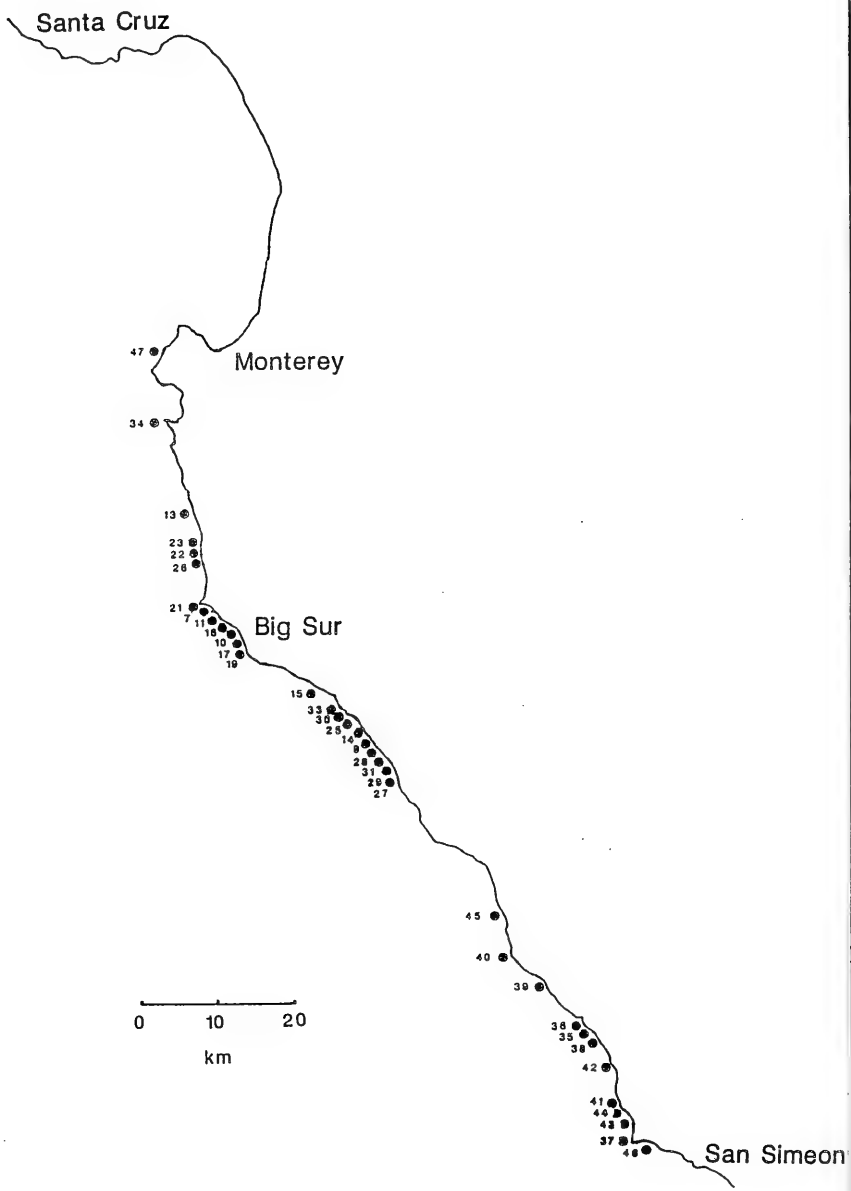


FIGURE 3.4 - The general north-south movement pattern of individual adult males, in relation to their average north-south location, over the monitoring period.

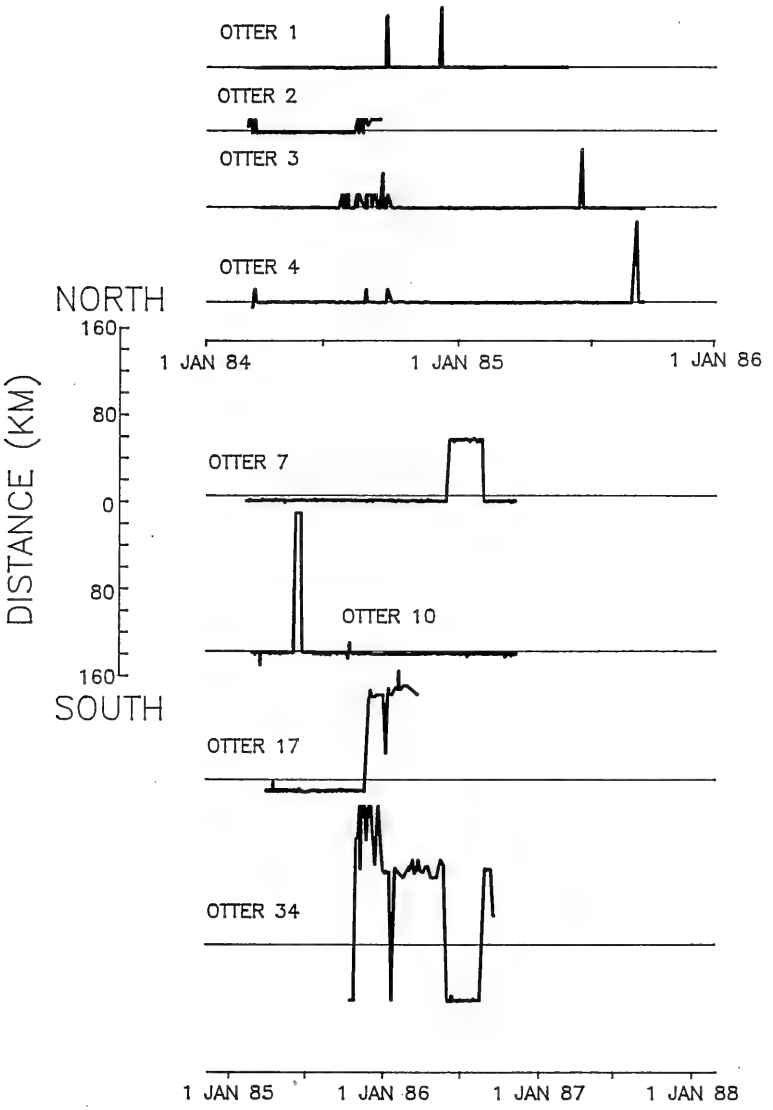


FIGURE 3.5 - The general north-south movement pattern of individual adult females, in relation to their average north-south location, over the monitoring period.

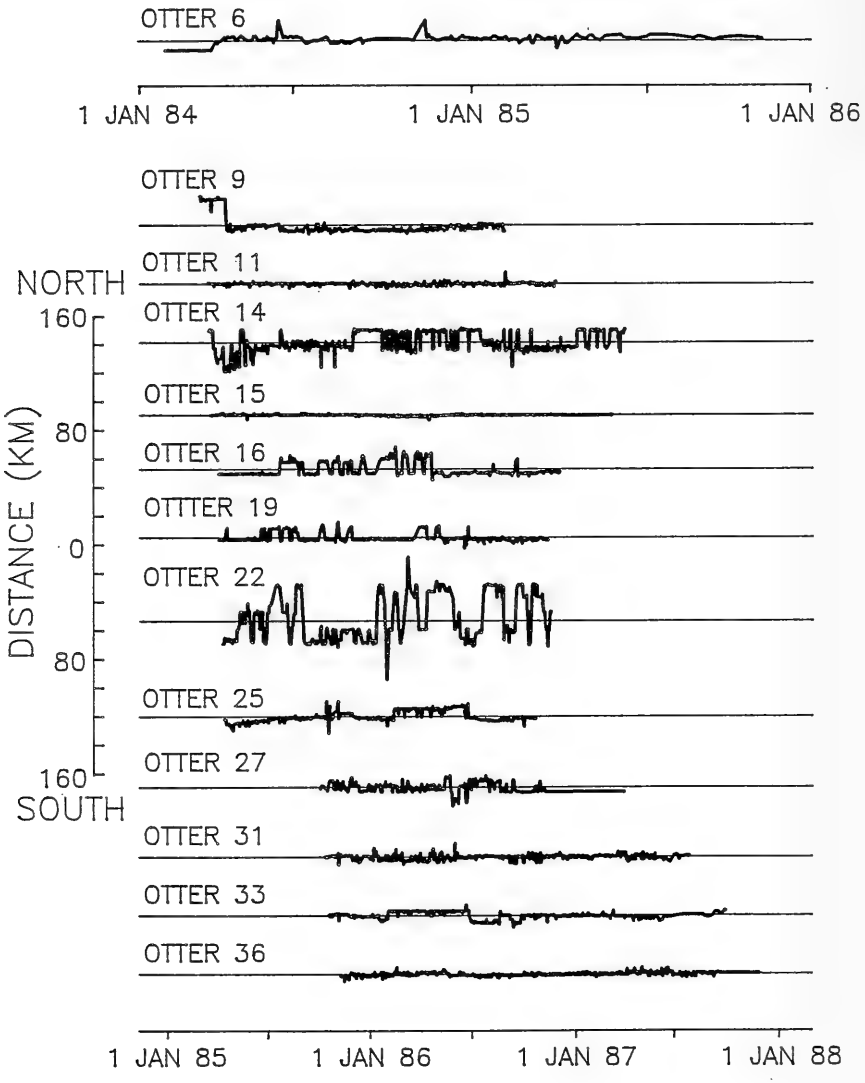


FIGURE 3.6 - The general north-south movement pattern of individual juvenile females, in relation to their average north-south location, over the monitoring period.

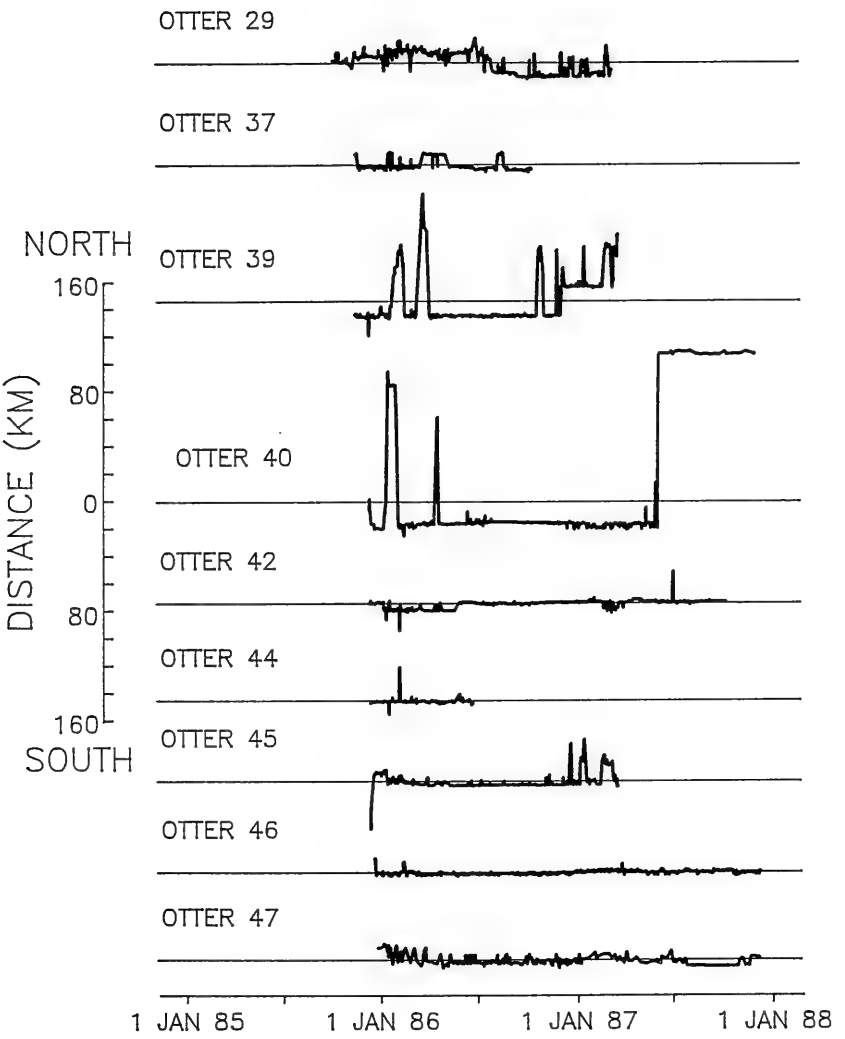
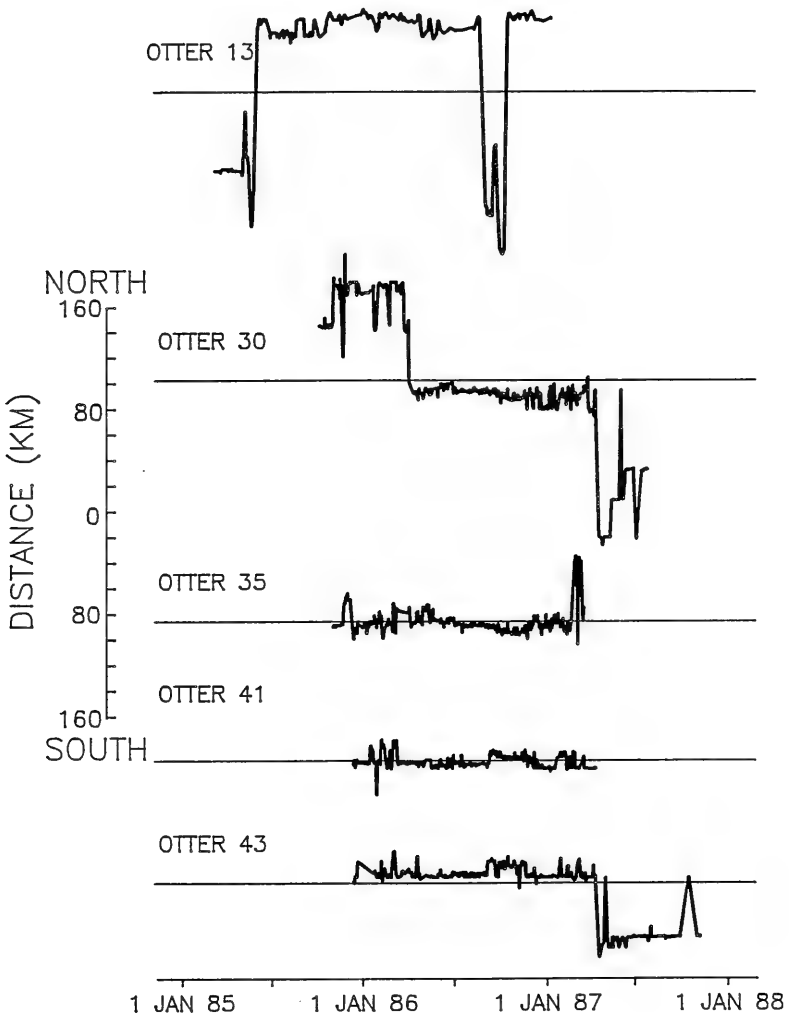


FIGURE 3.7 - The general north-south movement pattern of individual juvenile males, in relation to their average north-south location, over the monitoring period.



Four general movement patterns were apparent from these figures: 1) remaining within a small area throughout the study (for example, otters 11 and 46); 2) generally remaining within a small area but making occasional long-distance trips (otters 1 and 10); 3) shifting of centers of activity for extended periods of time (otters 17 and 30); and 4) frequent travel over long distances (otters 22 and 34).

Adult males captured in both "male areas" (otters 1-4) and "female areas" (otters 7, 10, 17, 23, and 34) sometimes made long-distance movements. These were often relatively brief "trips" to a new location, followed by a return to the

TABLE 3.3 - Area (ha) of daily home ranges based on data obtained during 24-hour watches in which locations were recorded once per hour. The areas were determined using the minimum area home range method (Hayne, 1949). AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

OTTER NUMBER	AGE/SEX	AREA (HA)
16	AF	10.33
36	AF	13.08
16	AF	22.52
36	AF	34.10
27	AF	58.23
19	AF	68.97
27	AF	227.59
29	AF	1166.35
34	AM	6.88
34	AM	12.75
7	AM	223.37
42	JF	31.69
42	JF	32.88
40	JF	107.03
40	JF	118.81
45	JF	119.29
47	JF	165.36
39	JF	212.53
47	JF	213.75
41	JM	221.24
35	JM	258.52
43	JM	302.14
35	JM	359.62
41	JM	379.49
30	JM	511.40
35	JM	570.23
30	JM	625.82
35	JM	666.38
41	JM	759.32

original location. No seasonal pattern was apparent in these "trips". Adult females tended to be more sedentary. However, two of them (otters 14 and 22) often moved distances on the order of 10 km within a short time.

Juvenile females tended to move more extensively than adult females and two of them (otters 39 and 40) made long-distance trips. Juvenile males tended to travel more than the other age/sex classes.

Distance offshore

Adult males and females were usually found relatively close to shore (Fig. 3.8). Adult females with pups were particularly close to shore. There was no apparent correlation between age of pup and distance offshore. The three females with pups in Figure 3.9 are (from left to right) otters 16, 27 and 36. The potential ages of their pups were in the ranges of 81 to 101, 6 to 17 and 0 to 37 days, respectively. Juveniles ranged farther from shore, and the tendency for the juvenile males to be much farther off-shore than individuals of the other age/sex classes was particularly striking. About four percent of our locations of juvenile males were over three km from shore.

In general, otters tended to feed slightly closer to shore than they rested but this was not true of all individuals (Fig. 3.9). Distance offshore was not closely related to time of day, although juvenile males were often relatively close to shore about 6 to 7 a.m. (Fig. 3.10).

Monthly harmonic mean ranges

The average monthly deviations from the harmonic mean center of the locations of the instrumented otters presented in Table 3.4 are plotted in Figure 3.11. These data reflect the general monthly movement patterns of the four age/sex classes. Monthly harmonic mean home range sizes of juveniles (Fig. 3.11) appeared to increase during the peak pupping months of February, March, and April, and during the secondary peak in August, September, and October (see Fig. 2.1). However, when monthly Hp were grouped into these six months of peak pupping vs. non-peak pupping seasons, no significant seasonal differences were detected by analysis of variance (Appendix 3.3). This lack of statistical significance, particularly among juvenile males, is probably because we monitored only a few juvenile males, there was great variation within individuals, and they had very small home range sizes in August (Fig. 3.11).

FIGURE 3.8 - The distribution of distances offshore for the four age/sex categories of adult females, adult males, juvenile females, and juvenile males.

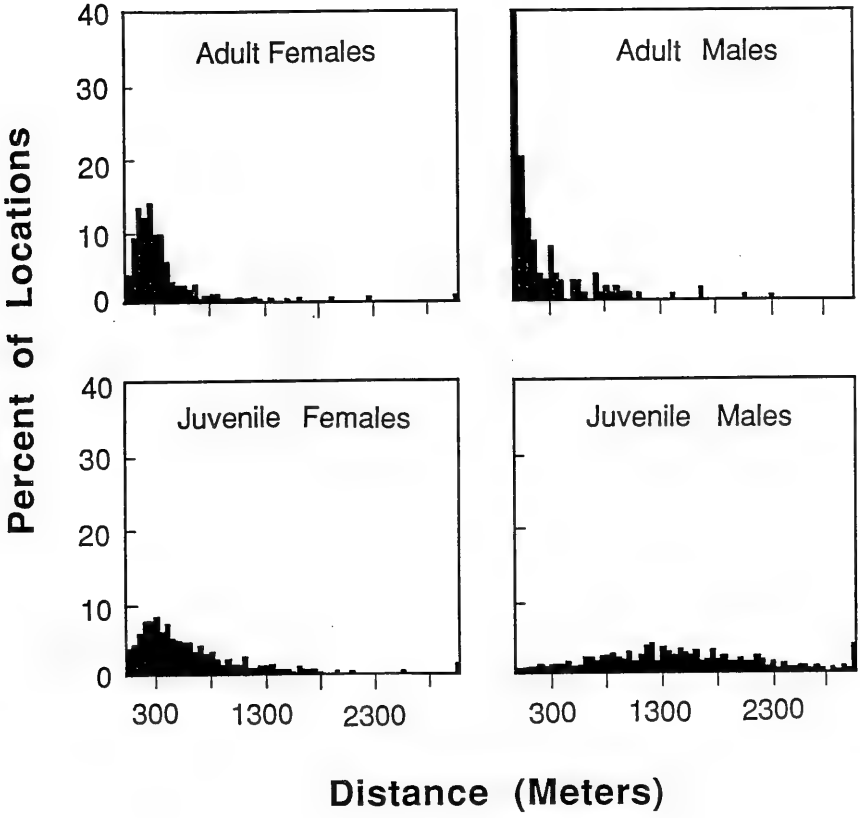


FIGURE 3.9 - The average distance off-shore while resting and feeding for individual otters partitioned by five age/sex categories of adult females, adult females with pups, adult males, juvenile females, and juvenile males.

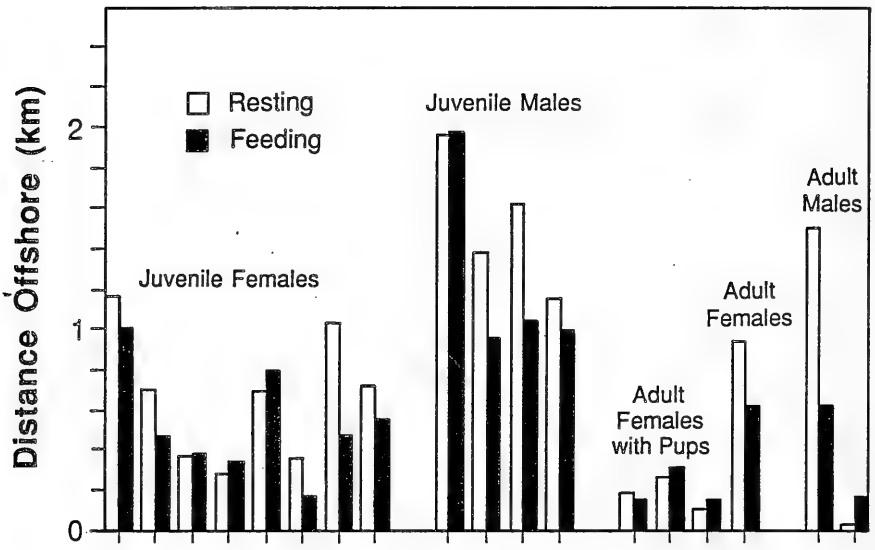


FIGURE 3.10 - The average distance off-shore for the various hours of the day for juvenile males and juvenile females.

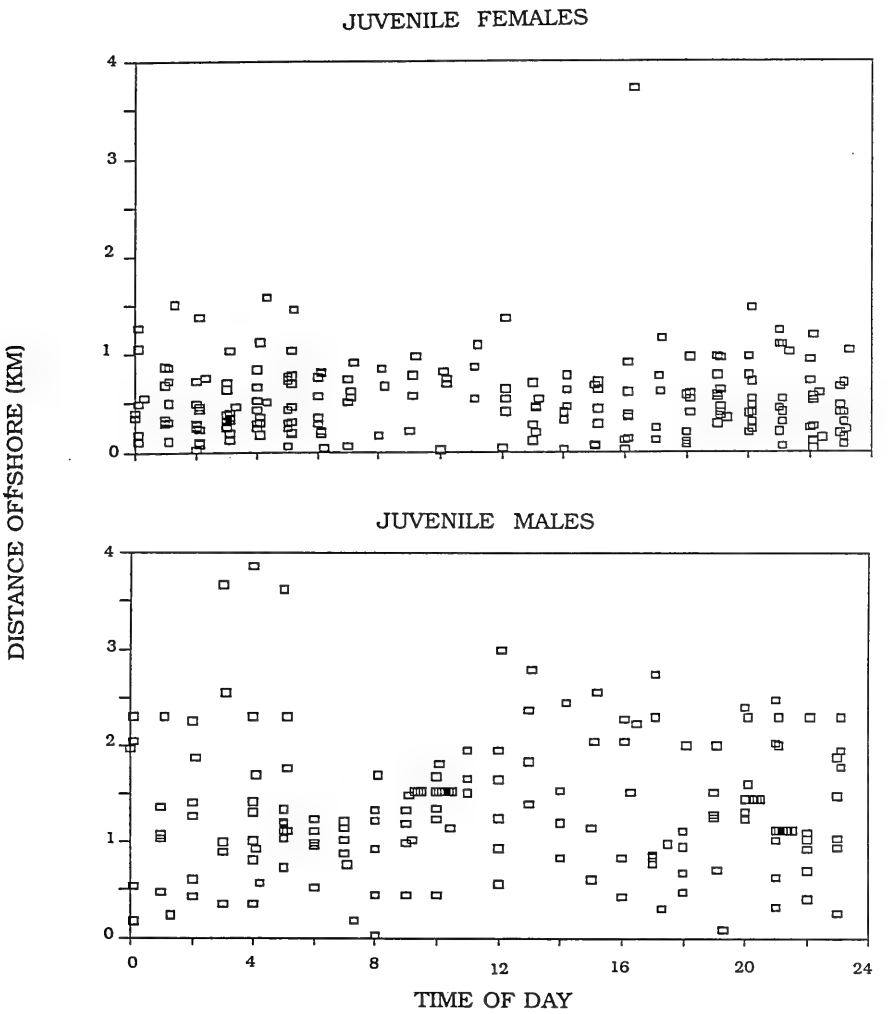


FIGURE 3.11 - The average distance deviation from the harmonic mean center of monthly home ranges for the four age/sex categories of adult females, adult males, juvenile females, and juvenile males.

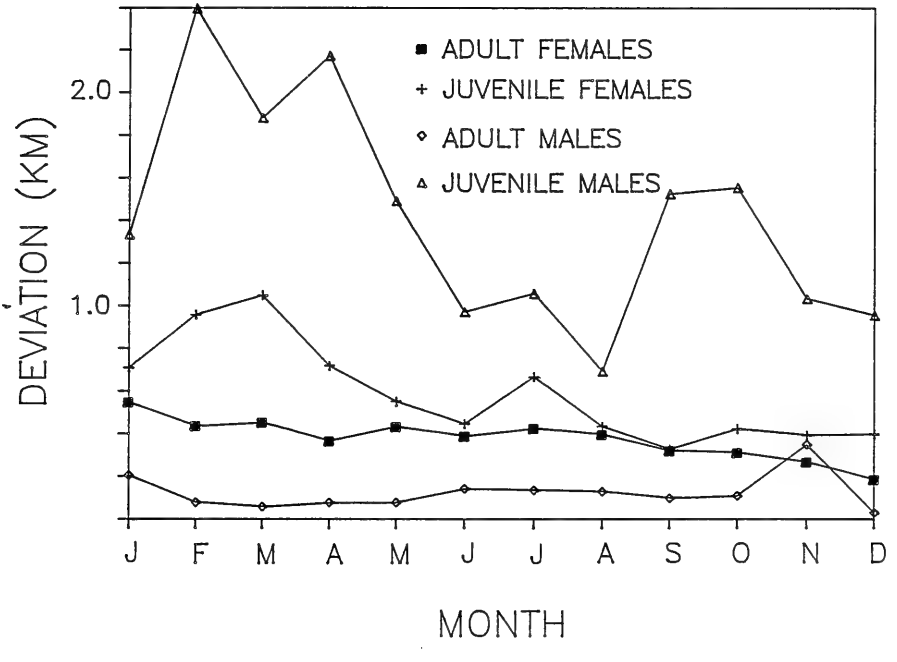


TABLE 3.4 - Average distance deviation (km) from the harmonic mean center of all locations for the four sex and age categories of adult males, adult females, juvenile females and juvenile males for each month of the year. AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

MONTH	AM		AF		JF		JM	
	MEAN	N	MEAN	N	MEAN	N	MEAN	N
JAN	0.207	7	0.623	13	0.810	10	1.418	5
FEB	0.079	7	0.472	13	1.170	10	2.288	6
MAR	0.059	10	0.478	17	0.984	10	1.433	5
APR	0.080	12	0.371	20	0.791	9	1.527	6
MAY	0.081	12	0.454	20	0.653	10	1.677	5
JUN	0.145	12	0.354	20	0.396	10	0.993	5
JUL	0.138	12	0.459	21	0.735	9	1.143	5
AUG	0.131	10	0.404	21	0.532	9	0.702	5
SEP	0.099	9	0.328	20	0.368	9	1.638	6
OCT	0.112	9	0.315	23	0.436	9	1.559	6
NOV	0.336	8	0.27	21	0.389	9	1.038	7
DEC	0.031	6	0.188	18	0.367	9	0.816	6

There was significant variation in monthly Hp among individuals of both adult sex classes but not for juveniles, whether seasonal effects were considered (Appendix 3.3) or not (Appendix 3.4). When seasonal effects were disregarded, variation of Hp among age/sex classes was much greater than variation among individuals within age/sex classes and was significant (Appendix 3.4). Adult males tended to move within a small area; adult females utilized areas slightly larger than those of adult males. Juveniles of both sexes traveled over larger areas than adults throughout the year, and juvenile males used strikingly larger areas than individuals of the other age/sex classes.

Distance between extreme locations

The average and two extreme locations, and the distance between these two extreme locations, for each otter are shown in Table 3.5 and plotted in Figure 3.12. Unlike Hp, the average distance between extreme locations is extremely sensitive to a few long-distance movements. Analysis of variance indicated that differences among age/sex classes were significant (Appendix 3.5), with juvenile males having the largest distances and adult females the smallest (Table 3.6). Distances for adult males, which occasionally take long-distance trips, were greater than those for adult and juvenile females.

These data are consistent with our other analyses of the movement data, indicating that juvenile males are the most extensive travelers.

FIGURE 3.12 - The distance between extreme locations for all of the instrumented sea otters in California, partitioned by the four age/sex categories of adult females, adult males, juvenile females, and juvenile males.

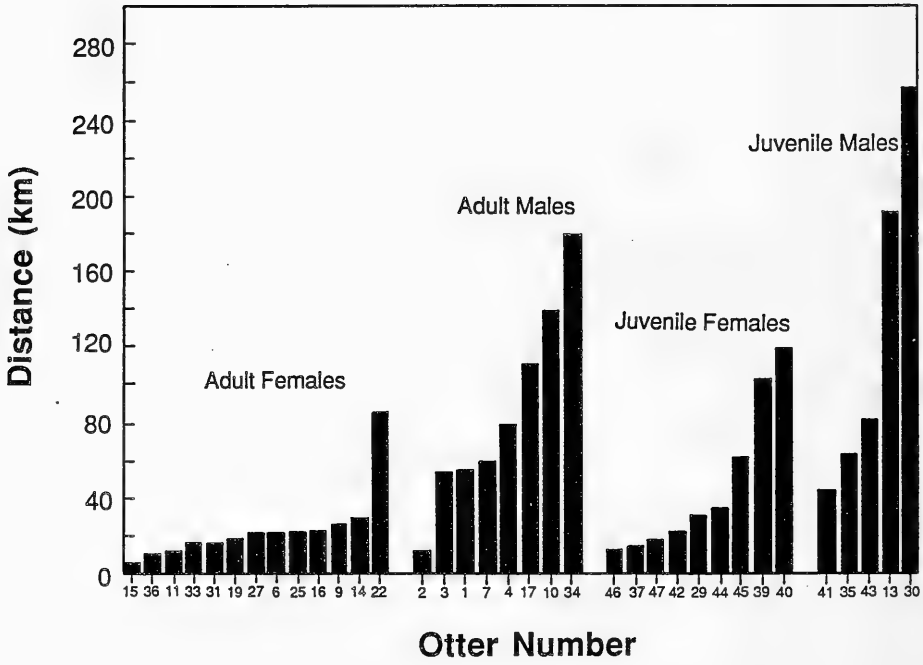


TABLE 3.5 - The average location along the five fathom line, and the northern-most and southern-most location along this line, that were recorded during the period of monitoring for each instrumented sea otter. AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

OTTER NO.	AGE/ SEX	MEAN LOCATION	NORTHERNMOST LOCATION (A)	SOUTHERNMOST LOCATION (B)	Distance Between A&B(km)
15	AF	COAST GALLERY	GRIMES POINT	PARTINGTON POINT	5.0
36	AF	SALMON CREEK	REDWOOD GULCH	RAGGED POINT	10.0
11	AF	FALSE SUR	VENTURA ROCKS	BIG SUR RIVER	11.5
33	AF	PARTINGTON PT	GRIMES POINT	ESALEN	15.5
31	AF	BUCK CREEK	TORRE CANYON	DOLAN ROCK	15.5
19	AF	WRECK BEACH	FALSE SUR	GRIMES POINT	18.5
27	AF	DOLAN ROCK	ANDERSON CANYON	LUCIA	21.5
6	AF	ARROYO LAGUNA	CHINA GULCH	LITTLE PICO CRK	21.5
25	AF	ANDERSON CR	GRIMES POINT	SQUARE BLACK ROCK	22.5
16	AF	PFEIFFER BEACH	LITTLE SUR RVR	GRIMES POINT	23.5
9	AF	BUCK CREEK	PFEIFFER POINT	DOLAN ROCK	26.5
14	AF	BUCK CREEK	GRIMES POINT	LUCIA	30.0
22	AF	ROCKY POINT	POINT PINOS	ANDERSON CANYON	86.0
2	AM	MORRO ROCK	CAYUCOS POINT	MORRO BAY	12.5
3	AM	MORRO ROCK	ARROYO LAGUNA	MORRO BAY	54.5
1	AM	MORRO ROCK	ARROYO LAGUNA	MORRO BAY	56.0
7	AM	POINT SUR	POINT PINOS	COOPER POINT	60.5
4	AM	MORRO ROCK	RAGGED PT INN	MONTANA DE ORO	79.5
17	AM	PFEIFFER BEACH	MOSS LANDING	COAST GALLERY	112.0
10	AM	PFEIFFER BEACH	SOQUEL POINT	TORRE CANYON	140.5
34	AM	SOBERANES PT	GREYHOUND ROCK	BUCK CREEK	181.0
46	JF	ARROYO LAGUNA	BECKETS REEF	SAN SIMEON POINT	13.0
37	JF	ARROYO LAGUNA	BECKETS REEF	SAN SIMEON POINT	15.0
47	JF	POINT JOE	MUSSEL POINT	SUNSET POINT	18.0
42	JF	RAGGED PT INN	COUNTY LINE	ARROYO LAGUNA	22.0
29	JF	DOLAN ROCK	COAST GALLERY	LUCIA	30.5
44	JF	BECKETS REEF	GORDA	ARROYO LAGUNA	34.5
45	JF	PLASKETT ROCK	DOLAN CREEK	BECKETS REEF	62.5
39	JF	SODA SPRING CR	POINT SUR	PIEDRAS BLANCAS	103.5
40	JF	CRUZ ROCK	VENTURA ROCKS	SAN SIMEON PT	120.0
41	JM	CRUZ ROCK	REDWOOD GULCH	SAN SIMEON CREEK	44.0
35	JM	COUNTY LINE	PACIFIC VALLEY	BECKETS REEF	64.0
43	JM	BECKETS REEF	SALMON CREEK	SAN SIMEON PT	82.0
13	JM	CARMEL BEACH	SUNSET BEACH	RAGGED PT INN	191.5
30	JM	JADE COVE	SOBERANES POINT	PIEDRAS BLANCAS	258.0

TABLE 3.6 - The average distance (km) between extreme locations, measured along the five fathom line, for the four sex and age categories of adult males, adult females, juvenile females and juvenile males. AF = Adult Female, AM = Adult Male, JF = Juvenile Female, JM = Juvenile Male.

AGE/SEX	MEAN (KM)	N	VARIANCE	RANGE (KM)
AF	23.65	13	368.28	5- 86
AM	97.71	7	2042.204	54-181
JF	46.56	9	1426.024	13-120
JM	127.90	5	6840.04	44-228

Because these data are based on the most extreme distances moved, they also show the tendency for adult males to make fairly long-distance trips. The one exception in Figure 3.12 is male number 2. However, he was monitored for only 100 days before he disappeared and it seems probable that he simply happened not to make a long trip within this relatively short monitoring period.

DISCUSSION

Radiotelemetry studies have shown that sea otter home ranges in Alaska consist of several heavily used areas connected by travel corridors (Garshelis and Garshelis, 1984; Chapter 8). The results of our studies in California agree with this general picture: otters tended to stay within a small area for an extended period and then suddenly move for a much greater distance.

Distance between successive daily locations

Otters of all age and sex classes were usually found within one or two km of their location on the previous day. There are no comparable data on the locations of individuals from one day to the next in the literature but Ribic (1982) measured the distance between successive locations of the same individual at 3.4-5 hour intervals. Some of Ribic's sample sizes were extremely small. However, if we compare our data to those data where she had samples of at least 10 locations, the distances reported in the two studies are similar.

This similarity suggests that sea otters have a tendency to move fairly quickly and directly between locations where a considerable amount of time is devoted to more sedentary activities such as resting or feeding. Such direct movements have been reported (Loughlin, 1980) and we often observed them during course of our study.

The longest distance between successive daily locations recorded in our study was about 47 km. This is similar to a movement of 48 km in 22 hours mentioned by Ribic (1982). Kenyon (1969) estimated that sea otters can swim at sustained speeds of about 2.5 km per hr., thus the long daily movements we recorded probably involved nearly constant swimming.

Long-distance movements

Other investigators have documented that sea otters make occasional long-distance movements (Kenyon, 1969; Ribic, 1982; Garshelis and Garshelis, 1984), but these were thought to largely reflect seasonal movements of males between summer and winter ranges. Our daily monitoring revealed that individual otters of all age/sex classes make a surprising number of long-distance movements at all times of year.

Although some individuals remained within a small area for extended periods, e.g. otter 7, an adult male that remained within a very small area for 18 months (Fig. 3.4), and otter 15, an adult female that visited only 5 km of coastline during the entire monitoring period (Fig. 3.5; Otter 15), it became evident to us that the longer an individual was monitored, the more likely it was to travel a significant distance. Only a few "trips" have been previously documented in the literature, probably because such long distance movements are less likely to be detected in tag-resight studies and radio telemetry studies of short duration. Although the reasons for these "trips" are unknown, it seems likely that they vary. Adult males may be seeking mating opportunities or areas with high-quality food resources. Juvenile males may be displaced by older males and may seek the company of other young males as well as high-quality food resources. Females, both juvenile and adult, that take extended "trips" may be looking for areas where they can become resident.

Seasonal patterns

We were unable to detect a significant seasonal pattern in the frequency of long-distance movements for any age/sex class, including adult males. We also looked for seasonal trends in the size of monthly harmonic mean home ranges. This method eliminates the possibility of greatly overestimating the area utilized due to a few long-distance movements. Once again, we failed to find any seasonal pattern in the size of the area used by adult males. However, we monitored only a small number of adult males. It also seems possible that predictable seasonal movements of adult males occur in some but not all areas. Juveniles appeared to show a seasonal pattern in harmonic mean home range size, with the peaks during the peaks of parturition period and pup dependency.

Although this effect was not statistically significant in our data set, it may nevertheless be a real phenomenon.

Variation within and among age/sex classes

We found substantial variation in movement patterns among individuals within all age/sex classes. For example, most adult females tended to be relatively sedentary but two of the 15 we monitored often traveled for considerable distances. In spite of this extensive individual variation, some generalizations on the movement patterns characteristic of the different age/sex classes are possible.

Measures that minimize the effects of long-distance movements, such as the distance between successive daily locations and monthly harmonic mean home ranges, indicate that, over the short-term, adult males tend to utilize smaller areas than adult females. This agrees with the findings of Loughlin (1980) and Ribic (1982) that adult females have larger home ranges than territorial or "resident" males. However, measures that are sensitive to long-distance movements, such as the distance between locations recorded at intervals of more than one day and the DBEL, show that adult males are more likely than adult females to make long-distance movements and thus tend to visit greater lengths of coastline over the long-term.

On a daily basis, movements of juvenile females were similar to those of adult females. However, juvenile females were more likely than adult females to make long-distance movements. Juvenile males tended to move for greater distances than the otters belonging to other age/sex classes on both a short- and long-term basis.

Distance offshore

It has been reported that otters in California rarely travel far offshore (Loughlin, 1980; Ribic, 1982). Estes and Jameson (1988) found that 90% of the otters observed from shore were within 600 m of the coast and that the probability of a shore-based observer sighting an otter was constant over observation distances of 50-850 m from shore, although it declined to zero by 1300 m. The majority of our locations of adult males and females and juvenile females were within 800 m of shore; however, the majority of our locations of juvenile males were over 800 meters from shore and over half of them were more than 1300 m (Figure 3.8). Although Estes and Jameson (1988) concluded that "few otters occurred at distances from shore beyond the observers' viewing ranges", our juvenile males were frequently located at distances beyond the viewing range of a shore-based observer.

Furthermore, our data underestimated the extent to which these juvenile males traveled offshore. The signal from an otter must be detectable from at least two shore locations to enable estimation of its distance offshore through triangulation. The signals of the juvenile males were often only faintly detectable from a single shore location; their distance offshore could not be estimated on these occasions. In addition, we were unable to locate the juvenile males a much larger proportion of the time than the other otters, probably because they often moved so far offshore that we could not receive their radio signals.

Home range size

Estimates of the area utilized by an individual otter are greatly influenced by whether or not long-distance movements by that individual were detected during the study period, whether or not they were included in the analysis if detected, and the specific method used to estimate the area utilized. The minimum convex polygon method is appropriate for measuring the areas used by otters in the intervals between long--distance movements; we used it to estimate the area used within a 24-hour period.

TABLE 3.7 - Comparison of home range areas (ha) for sea otters in California and Alaska calculated in this and previous studies.

AGE/SEX CLASS	LOCATION	AREA (HA)	SOURCE
Nonterritorial males	AK	400-1440	Garshelis&Garshelis 1984
Territorial males	CA	18-58	Loughlin 1980
Resident males	CA	80-460	Ribic 1982
Nonterritorial males	CA	29-138	Loughlin 1980
All males	CA	80-2980	Ribic 1982
Adult males	CA	7-223	This study
Juvenile males	CA	221-759	This study
All females	AK	20-960	Garshelis&Garshelis 1984
All females	CA	28-198	Loughlin 1980
Resident females	CA	470-680	Ribic 1982
All females	CA	470-2110	Ribic 1982
Adult females	CA	10-1166	This study
Juvenile females	CA	32-214	This study

Our estimates of the area used on a daily basis overlap estimates of home range size over longer periods made by other investigators (Table 3.7). This suggests that, in the intervals between long-distance trips, otters tend to travel on a daily basis over much of the area they are currently using. Because of the variety of methods used to calculate

the area utilized and the different periods of time included in the analyses, these estimates show great variance of home range size.

Early investigators suggested that there should be a relationship between home range size and metabolic rate (McNab, 1963). Because sea otters are known to have a high metabolic rate and are unable to fast for long, there may be a relationship between area used and prey availability in sea otters. However, such a relationship would be impossible to detect unless there is some standardization in methods of data collection and analysis. Greater consistency could be achieved by considering a rather short period, such as 24 hours, and excluding those periods in which individuals spent much of their time traveling between locations. Such comparisons might not be appropriate between areas in which the near-shore communities differed greatly.

The distance between extreme locations has been used as an index of home range size, particularly in Alaska (Garshelis and Garshelis, 1984; Chapter 8). In general, our values for adult males in California are greater than those reported for Alaska. There have been no reports of DBEL's over 100 km for instrumented otters in Alaska; three of our adult males in California had DBEL's of 112, 141, and 181 km. (Table 3.5). However, most of the Alaska data are from Garshelis and Garshelis (1984), who monitored instrumented otters for relatively short periods during the non-winter months, and it seems clear that this index, like measures of home range area, tends to increase with the length of time individuals are monitored. Although Garshelis and Garshelis (1984) did not document long-distance movements by any of their instrumented adult males, they observed that four tagged males moved about 100 km between their summer territories and a "male area" occupied during other times of the year. This suggests that the greatest distances visited by males in California and Alaska may be more similar than current telemetry data indicate.

DBEL's for adult females seem to be comparable in the two areas. Ours ranged from 5 to 86 km and those reported by Monnett and Rotterman for Alaskan females in Chapter 8 range from 28 to 80 km. Again, those reported by Garshelis and Garshelis (1984) were smaller, the largest being about 20 km.

Our data for juveniles are also similar to those of Monnett and Rotterman from Alaska (Chapter 8), in that males tended to move greater distances than females. Our DBEL's for juveniles of both sexes are much greater than for Alaska but the data are not entirely comparable. The Alaska data represent the movements of individuals instrumented as dependent pups and monitored through the early period of

independence, for a maximum of 21 months after weaning. Our data represent the movements of individuals captured after weaning. Some of these individuals appeared to be quite young but others were estimated, based on the cementum lines in their premolars, to be up to two years of age. In Alaska, the longest distance moved by a juvenile female was less than 50 km and that by a juvenile male was approximately 120 km (Chapter 8). Our longest distances were 120 km for a juvenile female and 258 km for a juvenile male. Although our juveniles moved farther, they were older.

In Alaska, juvenile males tended to move relatively long distances, which took them out of the areas occupied by reproductive adults, within a few weeks after weaning. It is not known if young males make similar movements in California soon after weaning, but the juvenile males we monitored remained in the area occupied by breeding adults for most of the study period. Many of them did associate with a male group that formed near Ragged Point, well within the "female area" for several months. Two of them finally moved into the "male area" in the southern part of the California range towards the end of the monitoring period.

Sex differences in dispersal patterns

Although the timing may differ, sex differences in dispersal patterns appear similar in California and Alaska. Sea otters exhibit the dispersal pattern typically found in polygynous mammals (Greenwood, 1980): juvenile males tend to move farther than females. The juvenile males ultimately join male groups, usually within "male areas", while juvenile females remain within their natal "female area".

Aggression from territorial males may play a role in the initial departure of the juvenile males from the kelp beds frequented by breeding adults. However, it is likely that, on the average, juvenile males ultimately benefit from this long distance dispersal in terms of increased reproductive success.

The extensive travels of juvenile males probably enable them to become familiar with a large area; this may be an advantage later in life, when, as young adults, they return to a "female" area and search for an available territory (Loughlin, 1980, Ribic, 1982). By participating in the frequent social interactions, such as various forms of play-fighting, that occur in male groups, juvenile males may gauge their strength relative to other males and develop the fighting skills needed to acquire a territory. Because male groups are often located in areas that have been occupied by sea otters for a shorter period than the "female" areas, juvenile males that join these groups may tend to derive

nutritional benefits. Increased prey availability during the male's growth period could have important benefits later in life, as the sexual dimorphism characteristic of sea otters, with males considerably larger than females, suggests that large body size is likely to be an advantage to males when fighting with other males.

In general, "female areas" have been occupied by otters for many years, and prey availability there is reduced compared to the "male areas". By remaining within these areas, juvenile females are forced to compete with larger, older otters for good foraging locations in an area that has already been exploited for some time. Our California data on time budgets and activity patterns (Chapter 4) and feeding patterns (Chapter 5) indicate that juvenile females tend to be poor competitors and their survival rates are rather low compared to other age/sex classes in both California (Chapter 2) and Alaska (Chapter 8 and 9).

Why then, do juvenile females remain in these "female areas"? Theory suggests that males will tend to behave so as to maximize mating opportunities and females so as to maximize the food resources available to them and their offspring. Juvenile females may ultimately benefit from acquiring a detailed familiarity with the distribution and availability of prey within a small area. In many mammals in which young females tend to remain within their natal area, female young may benefit by acquiring all or part of their mother's home range. The extent to which this occurs in sea otters is unknown. If adult females are intolerant of strange females, juvenile females that disperse from the "female" areas and subsequently return may have reduced chances of acquiring a good quality home range within these areas.

Regardless of the reasons for its occurrence, the sex difference in movement patterns of juvenile sea otters may have important consequences for sea otter population dynamics by decreasing survival of juvenile females (Chapter 2).

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CHAPTER 4

TIME BUDGETS AND ACTIVITY PATTERNS OF CALIFORNIA SEA OTTERS

K. RALLS AND D. B. SINIFF

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INTRODUCTION

The California sea otter population was reduced to a small number of animals by fur hunters in the 18th and 19th centuries. The remnant population grew at approximately five percent per year until sometime in the mid 1970's, when growth apparently ceased (Ralls, et al., 1983; Estes and Jameson, 1983; Estes, et al., 1986). A central question relating to the dynamics of the California sea otter population, and hence the development of a model for this population, is whether or not the recent lack of growth is due primarily to density independent factors, such as entanglement in gill nets (Wendell, et al., 1986) or attacks by sharks (Ames and Morejohn, 1980), primarily to density dependent factors, such as competition for food or other resources (Miller, 1980), or to both. However, the most recent surveys suggest that the population may have resumed growth (Jameson and Estes, 1988).

Several authors have proposed that time budgets might be useful as indicators of population status, assuming that food is an important limiting resource (Eberhardt, 1977; Estes, et al., 1982; Estes, et al., 1986). The prey available to sea otters varies with location and the length of time the area has been occupied by sea otters. Typically, most of the population initially consumes large prey items with high caloric content; as the availability of such prey decreases, the diet of the population diversifies to include smaller items and less preferred species (Estes, et al., 1981; Garshelis, et al., 1986). An otter should have to spend more time foraging to obtain a constant amount of energy in habitats with reduced abundance, size, or quality of prey than in those where high-quality food is abundant. Estes, et al., (1982) contrasted foraging patterns between two islands of the Aleutians; one where otters have existed for many years (Amchitka) and another that was recently colonized (Attu). The difference in time spent foraging (as determined by visual observations during the day) was dramatic as otters at Amchitka foraged during 55% of the daylight hours while those at Attu foraged only 17% of the daylight hours. Garshelis, et al., (1986) working in Prince William Sound, Alaska, assumed food was more abundant in areas that were recently invaded by sea otters and, under this assumption, confirmed the predicted relationship between food availability and the proportion of time devoted to foraging: otters spent about 10 percent more time foraging at Green Island, where sea otters had been present for many years, than in Nelson Bay, an area only recently reoccupied by sea otters where high quality prey items were abundant.

Time budgets in California have been determined primarily by visual observations of unidentified otters. The most recent study (Estes, et al., 1986) concluded that food was

probably not limiting further growth of the California population because sea otters there apparently foraged less than at Amchitka, there is unoccupied habitat at both ends of the range, and other mortality sources (e.g. gill nets) have been impacting the population. The use of radio-telemetry to collect time budget data has a number of advantages (Garshelis, et al., 1986) and is helpful in evaluating the many sources of mortality. Data can be collected over the entire 24-hour period and the time spent foraging can be estimated for individuals and age/sex classes, and direct data on sources of mortality are sometimes available.

One potential limitation of telemetry data is that the number of individuals monitored is often small. Thus, when the assumption is made that the instrumented individuals are representative of the population, the potential for bias, brought about by small sample size, exists. However, the ability to evaluate individual variation and compare age/sex groups allowed by this method greatly enhances the understanding of sources of variation. Further, visual scan samples also have biases because of differences in the spatial distribution among age/sex groups. For example, we found that juvenile males are often too far offshore to be seen, even with spotting scopes (Chap.3).

There have been two studies of sea otter time budgets in California based on telemetry. However, Ribic (1982) did not separate feeding from other kinds of activity and Loughlin's (1980) sample was small. Our data provide more extensive information on time budgets and activity patterns of California sea otters based on telemetry data.

METHODS

Radiotelemetry is particularly useful for collecting time budget and activity data on sea otters because radio signals are not transmitted through sea water. Because of this characteristic, the radio signal pattern varies according to an otter's activity. Three general categories of activity have been distinguished by listening to the radio signal from an otter: resting, feeding, and "other" (Loughlin, 1980; Garshelis, et al., 1986). The radio signal from an otter resting on the surface of the water is constant. Most foraging otters alternately dive to obtain prey and return to the surface to consume their catch, or if they were unsuccessful, breathe before diving again. Thus the radio signal of a feeding otter is usually a characteristic pattern of alternating periods of signal and silence. When otters are engaged in activities other than resting or feeding, such as swimming, vigorous grooming, or social interactions, the signal is variable, with the strength of each signal depending upon the orientation of the otter's body with respect to the

surface of the water. We called this category "other". When the otter could be seen, specific behaviors such as swimming, active grooming, or social interactions were recorded. These behaviors were later combined into the "other" category so that the data collected visually would be comparable to data based solely on the radio signal. A potential bias in California was the very shallow feeding within the kelp canopy that might be confused with the "other" category. This was evaluated by comparisons with visual observations.

In preliminary analyses, we distinguished a fourth activity category, "unknown", not used in other telemetry studies of 24-hour activity (Loughlin, 1980; Garshelis, et al., 1986), for those data points where the observer could tell from the radio signal that the otter was active but was not certain whether or not it was feeding, and those in which the radio signal was so weak that the activity could not be identified.

We directly compared activity data collected visually with those obtained only by listening to the radio signal without seeing the otter. Two observers, one using each method, simultaneously recorded data on the same animal at five-minute intervals. These data were collected by several different pairs of observers on a variety of individual otters.

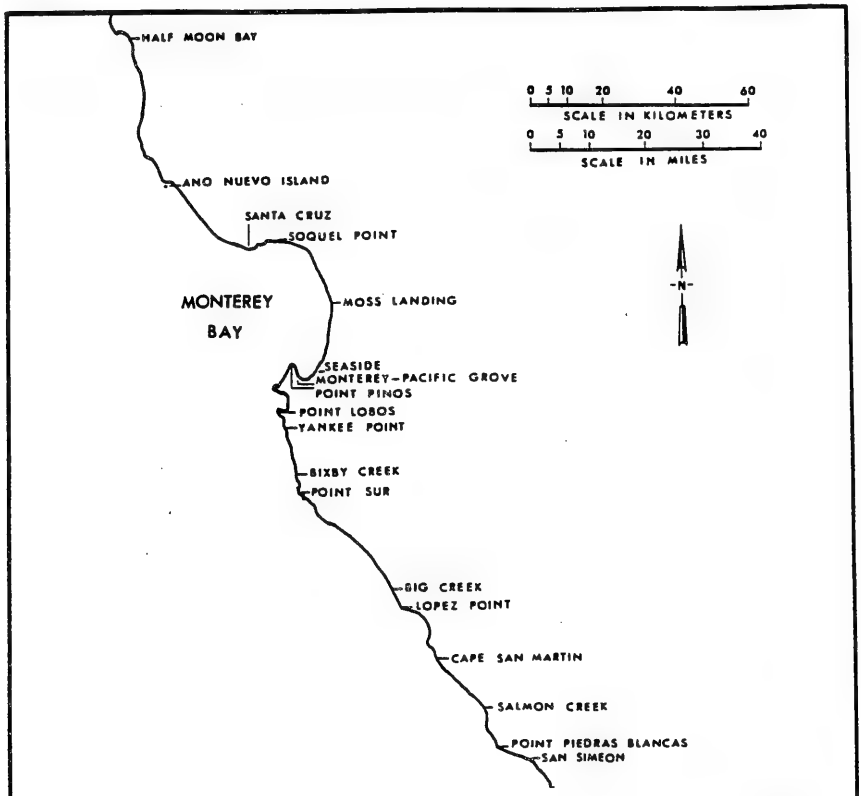
A team of 3 to 4 people, each taking a 6 to 10 hour shift, monitored the activity of individual otters for one or more 24-hour periods. Most data-collection periods were either 24 or 48 hours in length (Appendix 4.1). Data were recorded at 10-min intervals. We developed these methods by trying various alternatives on otters 1-4 in Morro Bay. Our activity data on these otters are thus not directly comparable to the majority of our data and are not included in our analyses of time budgets. Thus, the data that were included in our analyses of time budgets mostly came from the center of the California sea otter range. Fig. 4.1 shows the relative locations of the watches. Considering the locations of these watches and the number of individuals that we were able to monitor for each age/sex class, we feel that we had a representative sample of sea otter activity in areas that had been occupied for a long period of time.

RESULTS

Activity in relation to time of day

Otters of all age/sex classes tended to be active and feed for a large proportion of time during the late afternoon and early evening but there were differences in the activity patterns of various groups. For adult males in Morro Bay, we plotted only periods of activity and inactivity: these animals

FIGURE 4.1 -- The locations along the California coast of watches for collecting time budget data on sea otters instrumented with radio transmitters.



Location of watch	Adults		Juveniles	
	Females	Males	Females	Males
Santa Cruz - Moss Landing	0	0	0	1
Moss Landing - Point Sur	1	1	1	0
Point Sur - Cape San Martin	27	7	2	0
Cape San Martin - San Simeon	8	0	9	7

had a clearly bimodal activity pattern with a second major activity period in the morning, peaking about 8 a.m. (Fig. 4.2a). A similar early morning peak, in the percentage of time feeding, was noticeable in the juvenile males (Fig. 4.3a), the adult females (Fig. 4.4a), and the adult females with pups (Fig. 4.4b). The evening feeding peak for the adult males in the Big Sur area was so large that their pattern was almost unimodal (Fig. 4.2b). The juvenile females had a much broader feeding peak than any of the other groups, feeding about 50% of the time even in the middle of the day when the other age/sex groups rested (Fig. 4.3b). In contrast to the other groups, the juvenile females often rested during the night, from midnight to seven a.m.

There was a good deal of variation between individuals, but also variation from one day to the next, at the same time of day, for each individual. Our sample sizes, at a specific time of day, were not large enough to statistically test the significance of these sources of variance, since most individuals had only three to four data points for a given hour of the day.

Comparison of visually and telemetrically collected data

Our data provide the first formal comparison of visual and telemetric estimates of otter activity in which feeding was distinguished as a separate category, as neither Loughlin (1982) nor Garshelis, et al., (1986) undertook such a comparison. Ribic (1982) found good agreement between visual and telemetric data when only active and inactive were scored.

We found the highest agreement between the methods when an otter was resting: when the visual observer indicated that an otter was resting, the telemetric data agreed 93 percent of the time (Table 4.1). The telemetric observer never scored resting as feeding or "unknown" but occasionally scored it as "other". This error tended to occur when sea conditions such as high swell caused the otter to move about even though it was resting.

When the visual observer indicated that an otter was feeding, the telemetric data agreed 88 percent of the time (Table 4.1). The telemetric observer rarely scored feeding as resting or "other" but did sometimes indicate that the otter's activity was "unknown". This tended to occur when an otter was feeding without making regular dives. Otters in California can forage in kelp for prey items such as kelp crabs or obtain small items such as mussels from rocks without remaining submerged for more than a few seconds.

When the visual observer indicated that an otter was engaged in "other" activities, the telemetric data agreed only

FIGURE 4.2 -- The percent of time that adult male sea otters spent in various activities at the various hours of the day. Males in the Morro Bay area of California are shown in the upper graph; the males located in the Big Sur area are shown in the lower figure.

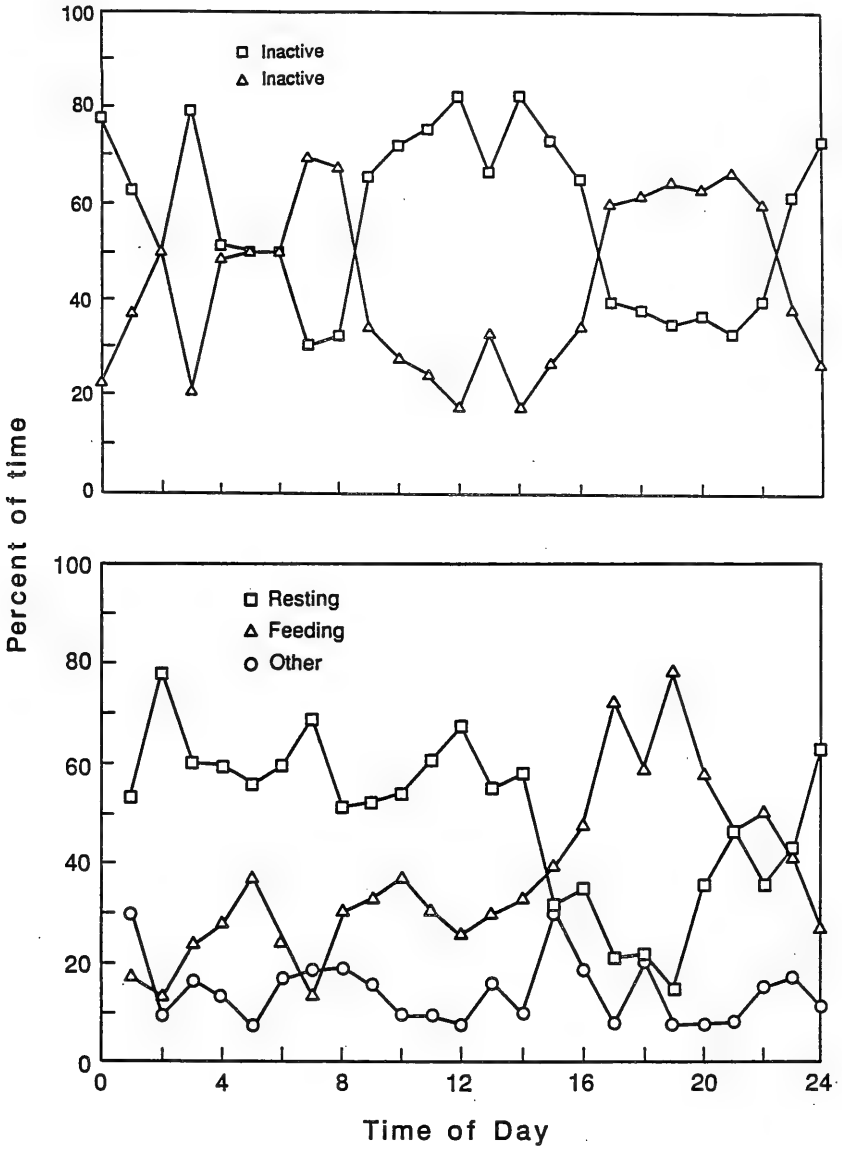


FIGURE 4.3 -- The percent of time that instrumented juvenile sea otters in California spent resting, feeding and in "other" activity at the various times of the day. Data for juvenile males are shown in the upper graph and those for juvenile females in the lower graph.

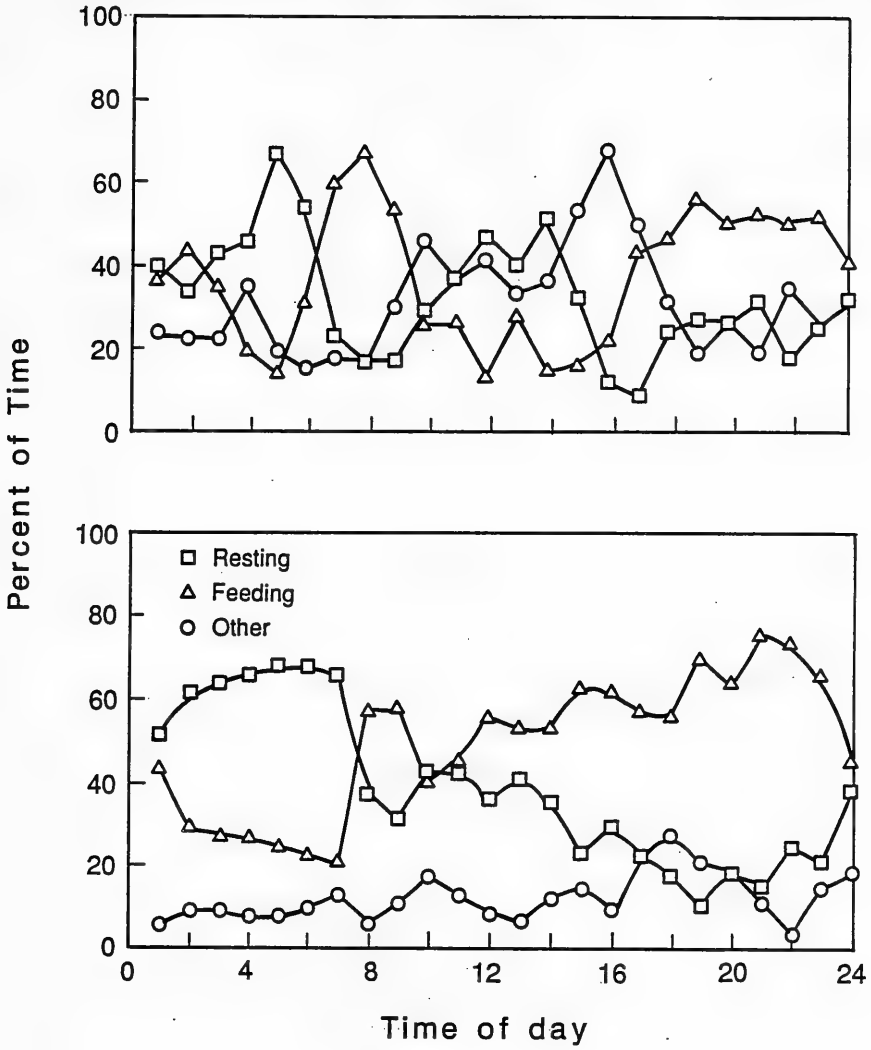


FIGURE 4.4 -- The percent of time that adult female sea otters in California spent resting, feeding and in "other" activity at the various hours of the day. Data for adult females without pups are shown in the upper graph and data for adult females with pups in the lower graph.

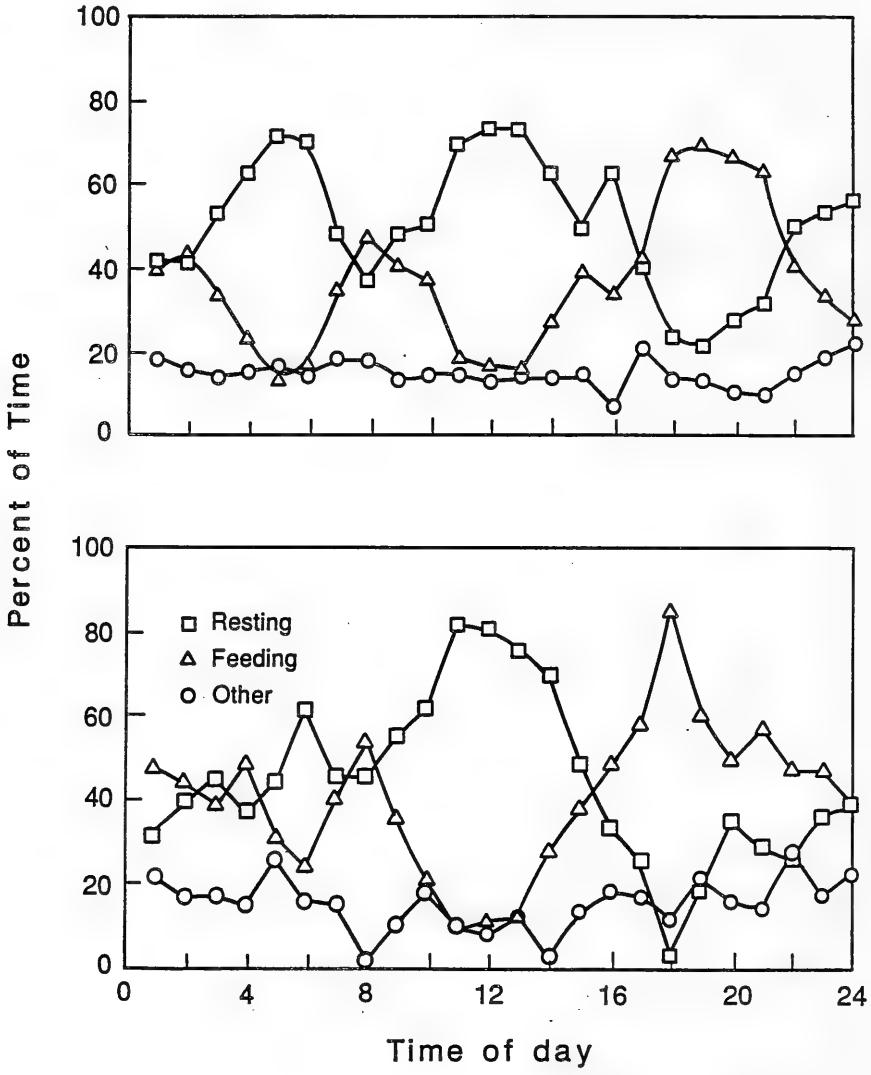


TABLE 4.1 - A comparison between activity data obtained visually with those obtained using the quality of the telemetric signal. The numbers in this table represent the number of 5-minute sampling periods where the activity of an otter was determined. These observations were taken simultaneously by two independent observers. AF = adult female without pup; AFP = adult female with pup; JF = juvenile female; JM = juvenile male.

		NUMBER OF FIVE-MINUTE SAMPLE PERIODS					
		Visual Observer	Telemetry observer				Percent Agree.
DATE		REST	REST	FEED	OTHER	UNKNOWN	
31-May-85	AF	38	36	2			
04-Feb-87	AF	32	31		1		
05-Feb-87	AFP	15	15				
25-Feb-87	AF	7	6		1		
27-Feb-87	JM	1		1			
27-Feb-87	JF	24	20		4		
03-Mar-87	AF	1	1				
30-Mar-87	AFP	12	12				
TOTAL		130	121				93
		FEED	REST	FEED	OTHER	UNKNOWN	
31-May-85	AF	33	33				
14-Feb-87	AFP	8	1	6	1		
25-Feb-87	AF	19	11		8		
27-Feb-87	JM	3		3			
27-Feb-87	JF	3	3				
02-Mar-87	JF	43	41		2		
03-Mar-87	AF	5	5				
07-Apr-87	AF	8	8				
TOTAL			122	107			88
		OTHER	REST	FEED	OTHER	UNKNOWN	
31-May-85	AF	2	1	1			
14-Feb-87	AFP	2	2				
25-Feb-87	AF	2	1		1		
27-Feb-87	JM	10	9	1			
27-Feb-87	JF	7	2		5		
30-Mar-87	AFP	1	1				
TOTAL			24		15		63

63 percent of the time. Activities in the "other" category were rarely recorded as feeding by the telemetric observer but were sometimes scored as resting or "unknown". "Other" was most commonly recorded as "resting" when the otter was grooming fairly vigorously without submerging the main part of its body.

TABLE 4.2 - A comparison between time budgets calculated from observing activity visually and judging activity using the quality of telemetric signal.

	Number of 5-min periods		Percentage of time	
	Visual	Telemetry	Visual	Telemetry
REST	130	121	47	44
FEED	122	108	44	39
OTHER	24	25	9	9
UNKNOWN	0	16	0	6

A comparison of the overall time budgets based on the visual and telemetric data collected simultaneously on the same otters (presented in Table 4.1) indicated that the telemetric data underestimated resting by 3 percent and feeding by 5 percent for this particular data set (Table 4.2). These data provide only an indication of the differences between estimates based on the two methods. The magnitude of the differences will vary with such factors as the sea state during the period of data collection, the extent to which the otter being studied feeds without making regular dives, and the individuals recording the data. Although these data suggest that we underestimated the proportion of time spent feeding, it would be inappropriate to simply increase our estimates of the overall proportion of time spent feeding by five percent because of this variation and because our estimates are based on a combination of visual and telemetrically collected data.

Time budgets

Using the entire data set collected during the 24 to 72-hour watches (Appendix 4.1), we assessed the extent to which different ways of handling the "unknown" data might affect our results by comparing four ways of treating them. These were: 1) including them in the "other" category, as in our previous reports (Ralls, et al., 1985; Siniff and Ralls, 1986); 2) keeping them as a separate category; 3) excluding them from the analysis; and 4) including them in the "feeding" category to get an estimate of the maximum possible feeding time, as our data suggest that much of the "unknown" category may be feeding. Because the "unknown" category was small, ranging from 1 to 7 percent of the total time, the various ways of treating this category had relatively little effect on our estimations of the percentages of time the different age/sex classes of otters spent resting and feeding (Table 4.3). We therefore included the "unknown" data in the "other" category in subsequent analyses.

We tested differences in average percent of time spent feeding among sex and age classes using analysis of variance for the percent of time feeding for each individual monitored for 24-hour activity data. The results of this analysis, using Scheffe's multiple comparison test for difference among sex/age classes, showed that juvenile females fed significantly more than adult females, adult males and juvenile males, but not more than adult females with pups ($p < .05$) (Table 4.4). Females with small pups fed more than females with large pups but this difference was not significant (Table 4.5).

To facilitate a comparison of our data to data collected visually (Estes, et al., 1986), we tabulated the number of ten-minute periods devoted to "resting", "feeding" and "other" for each observation period in three ways: 1) for all data recorded during that observation period (Appendix 4.1); 2) for those data recorded during daylight hours (defined as 1/2 hour before sunrise to 1/2 hour after sunset)(Appendix 4.2); and 3) for those data recorded while the otter could be seen (Appendix 4.3).

The various age/sex classes of otters spent about the same percentages of time resting and feeding during daylight hours (Table 4.6) as they did over the entire 24-hour period. When only the data collected visually were considered, juvenile females still fed more than adult males and adult females (Table 4.6); juvenile females and adult males fed a greater, and adult females a smaller percentage of the time than indicated in the other two data sets. Insufficient visual data were collected on juvenile males and adult females with pups to allow a comparison of these groups. Comparisons of coefficients of variation (for the means of individuals for each sex/age category for the given method of data collection) indicated that the data collected visually were the most variable and those collected over the complete 24--hour period the least variable (Table 4.6).

DISCUSSION

Activity in relation to time of day

Sea otter activity patterns can be affected by a variety of factors including geographical location, weather, season, available prey, and age/sex class (Garshelis, 1983, Estes et al., 1986). Otters in California tend to be crepuscular, resting mainly in the middle of the day (Ribic, 1982; Loughlin, 1980; our data); although Estes, et al., found that

TABLE 4.3 - A comparison among the methods of calculating time budgets. The unknown data are classified by four different methods: including them in the "other" category, separating them as unknown, excluding them, and including them in "feeding". OP = observation periods, AM = adult male. Other abbreviations as in Table 4.1.

TREATMENT OF UNKNOWN DATA	AGE/SEX CLASS	PERCENTAGE OF TIME Rest	Feed	Other	Unknown	SAMPLE SIZES Otters	Hours	OP
AS OTHER	AF	48	37	15	--	8	830	28
AS UNKNOWN		48	36	8	7			
EXCLUDED		52	37	9	--			
AS FEEDING		48	43	8	--			
AS OTHER	AFP	45	39	16	--	6	264	8
AS UNKNOWN		44	39	11	4			
EXCLUDED		46	41	12	--			
AS FEEDING		44	43	11	--			
AS OTHER	AM	50	36	14	--	4	216	7
AS UNKNOWN		50	37	9	4			
EXCLUDED		52	38	9	--			
AS FEEDING		50	41	9	--			
AS OTHER	JF	40	48	12	--	9	417	12
AS UNKNOWN		40	49	10	1			
EXCLUDED		40	49	10	--			
AS FEEDING		40	50	10	--			
AS OTHER	JM	34	37	29	--	5	218	8
AS UNKNOWN		34	37	24	4			
EXCLUDED		35	39	26	--			
AS FEEDING		34	41	24	--			

TABLE 4.4 - Analysis of variance testing for differences in percent of time spent feeding between the various sex/age classes.

Source	d.f.	S.S.	M.S.	F
Among sex/age classes	4	956	426.8	10.7
Error	24	1707	39.8	

Test of means (% of time feeding)

JF	AFP	AM	JM	AF
48	39			
		36	37	37

Means underlined by the same line are not significantly different ($p<.05$; Scheffe's test).

TABLE 4.5 - A comparison of time budgets between females that were accompanied by small pups and those accompanied by large pups.

ACTIVITY	MEAN PERCENTAGE OF TIME	VARIANCE	NUMBER OF OBSERVATION PERIODS
	FEMALES WITH SMALL PUPS		
Rest	40.60	257.30	4
Feed	42.71	194.80	4
Other	16.53	12.29	4
	FEMALES WITH LARGE PUPS		
Rest	48.45	17.97	3
Feed	36.02	104.70	3
Other	15.53	39.38	3

Table 4.6 - A comparison of the percent of time spent in each of the three activity categories, resting, feeding and other, for activity data collected over the entire 24-hour period, for daylight data only, and for visual data, for the age/sex categories of adult females, adult females with pups, adult males, juvenile females, and juvenile males.

	ENTIRE 24-HR PERIOD		DAYLIGHT ONLY		VISUAL DATA	
	MEAN	NO.OBS.*	MEAN	NO.OBS.*	MEAN	NO.OBS.*
			ADULT FEMALES			
Rest	48.2	28	47.72	28	54.4	24
Feed	36.8	28	38.10	28	28.0	24
Other	15.0	28	14.18	28	17.7	24
			ADULT FEMALES WITH PUPS			
Rest	44.52	8	46.99	8		
Feed	39.39	8	39.29	8		
Other	16.09	8	13.71	8		
			ADULT MALES			
Rest	50.43	7	47.54	7	43.6	5
Feed	35.8	7	38.06	7	41.2	5
Other	13.77	7	14.40	7	14.6	5
			JUVENILE FEMALES			
Rest	39.76	12	34.83	12	38.5	11
Feed	47.81	12	51.61	12	57.8	11
Other	12.43	12	13.56	12	3.7	11
			JUVENILE MALES			
Rest	33.96	8	28.44	8		
Feed	36.84	8	37.15	8		
Other	29.20	8	34.42	8		

*NUMBER OF OBSERVATION PERIODS

the otters in one of the areas they sampled had no apparent 24-hour pattern. Garshelis (1983) found deviations from the crepuscular pattern when locally preferred prey tended to be active at night. Also, he suggested that, in Alaska, short day lengths and poor weather conditions, combined with poor resources, may have made it impossible for otters to maintain body temperature during long rest periods. It might seem less likely that this would occur in the milder California climate; however, one of our juvenile females was observed shivering on several occasions before she disappeared and presumably died. Estes, et al., (1986) suggested that environmental factors such as wind and waves may disrupt the 24-hour pattern in California. Although we found that otters of all age/sex classes in California did some feeding at night, none fed primarily at night as did male otters at one location in Alaska where the preferred prey was dungeness crabs, which are thought to be more active, and hence more vulnerable, at night (Garshelis, et al., 1986). Because we did not collect activity data in extremely bad weather, we were unable to determine whether or not otters in California rest for shorter periods at midday under such conditions.

In contrast to the other age/sex classes, juvenile females tended to rest for the greatest proportion of the time from midnight to eight in the morning rather than feed. Thus, for our data the juvenile females departed most from the more usual crepuscular pattern. Sea otters are known to steal food from other individuals (Fisher, 1939; pers. obs), and we observed that juvenile females were the group from which food was often taken. Perhaps they tend to feed at different times than the majority of their conspecifics to reduce the risk of losing prey in this manner.

Time budgets in relation to other studies

As Ribic (1982) did not separate feeding from other kinds of activity, Loughlin's (1980) telemetry data on six otters in Monterey Bay are the only California data comparable to ours. Our data on adult males and females are very similar to Loughlin's data in spite of his small sample size, the different study areas and the number of years between the two studies (Table 4.7). Garshelis, et al., (1986) present time budget data based on telemetry for sea otters from two localities in Prince William Sound, Alaska: Green Island and Nelson Bay. Sea otters had been present in the Green Island area since the 1950's or earlier. Females remained in this area throughout the year; males visited for various periods of time during the breeding season. In contrast, otters had moved into Nelson Bay fairly recently. Most of the otters there were males, some of which moved seasonally to breeding areas such as Green Island. Both adult males and females fed significantly less time at Nelson Bay, where large, high

quality prey such as clams and crabs were easily available, than at Green Island, where such items were rare.

TABLE 4.7 - A comparison of the activity budgets for sea otters calculated in this study and those in the literature.

AGE/SEX CLASS	LOCATION	METHOD	PERCENTAGE OF TIME Rest	Feed	Other	REFERENCE
AM	CALIF.	TELEMETRY	57	33	10	Loughlin 1979
AF	CALIF.	TELEMETRY	50	36	14	Loughlin 1979
AM	CALIF.	TELEMETRY	50	36	14	This study
AF	CALIF.	TELEMETRY	48	37	15	This study
AFP	CALIF.	TELEMETRY	45	39	16	This study
JM	CALIF.	TELEMETRY	34	37	29	This study
JF	CALIF.	TELEMETRY	40	48	13	This study
UNKNOWN	CALIF.	VISUAL	53-63	21-28	9-22	Estes, et al., 1986
M	AK**	TELEMETRY	50	47	3	Garshelis***
AF	AK**	TELEMETRY	50	47	3	Garshelis***
AFP	AK**	TELEMETRY	43	53	3	Garshelis***
PUPS*	AK**	TELEMETRY	45	51	4	Garshelis***
M	AK****	TELEMETRY	49	37	15	Garshelis***
AF	AK****	TELEMETRY	51	37	12	Garshelis***

*Independent pups
**GREEN ISLAND(Alaska)
***Garshelis, et al., 1986 (reference)
****NELSON BAY (Alaska)

Our data were collected in the central portion of the sea otter range in California, in areas where sea otters have been present for many years. The general patterns in our data were the same as those at Green Island, Alaska, where otters have also been established for a long time. At Green Island, adult males and females fed for about the same percentage of time and females with pups fed slightly more than females without pups. At Green Island, recently weaned, independent pups fed more than adults. Juvenile males in California fed about the same amount of time as adults, but juvenile females fed more than adults, except for females with pups.

Estes, et al., (1986) estimated the proportion of time spent foraging by scan sampling (Altmann, 1974) the otters visible along the California coastline from dawn to dusk at 1/2 hour intervals and recording the activity of each otter observed. Estimates of the proportion of time spent feeding based on this technique are lower than those based on

radiotelemetry (Table 4.7). If otters in California spend a higher proportion of their feeding during the night than during the day, then scan samples during the day would tend to underestimate the proportion of time spent feeding. Garshelis, et al., (1986) found that, in some areas of Alaska, otters do feed mainly during the night. However, we found no difference in the proportion of time spent feeding during daylight hours and that over the entire 24-hour day. The most probable explanation for the difference between the scan sample and telemetry data is that feeding otters have a lower probability of being seen than resting otters (Estes and Jameson, 1988), and are thus more often missed during scan samples.

Time budgets as indicators of population status

Estes, et al., (1986) concluded that further growth, in recent years, of the California population was not because of food limitation, primarily because their estimates of the proportion of time the population spent foraging were similar to those of populations in Alaska known to be below equilibrium density. However, when all the available data are considered (Table 4.7) it seems likely that their scan sampling data underestimated the time spent feeding. Certainly, other factors than food availability, such as accidental capture in gill-nets, have contributed to the reduced growth of the California sea otter population (Wendell, et al., 1986). Further, time budgets may be affected by factors other than the prey availability, such as weather conditions, prey type, and study methods that obtain data in different ways. It seems likely that the best comparisons of activity data are those between studies based on telemetry methods. We did not collect data during bad weather. Garshelis, et al., (1986) were able to use automatic recording to obtain data during bad weather in Alaska, and found that otters fed more during such periods. Thus, we probably underestimated the proportion of time California otters spend feeding. Nevertheless, we found juvenile females fed at least 48 percent of the time; which represents a substantial effort when compared to any existing activity data.

They also tended to have longer feeding bouts than otters in the other age/sex classes, although the intervals between these bouts were about the same as in the other classes (Chapter 5). Two of our juvenile female otters (numbers 44 and 46) had their prey stolen repeatedly. The prey stealing was selective: only large desirable items were stolen. Otters whose prey is stolen may temporarily stop foraging, move to another location, or capture apparently less desirable species of prey. Otter 44 subsequently died: her stomach was empty although there were shells in her intestine. The only otter

in our study that regularly hauled out was another juvenile female (otter 42). Hauling-out is a behavior that may help to conserve energy (Garshelis, 1983).

Differences in the ability of members of different age/sex classes to compete for food resources are common in vertebrates (Sutherland and Parker, 1985; Clutton-Brock and Albon, 1985; Dunbar, 1985). Because of these differences in competitive ability, the effects of food shortage are usually concentrated on particular individuals. If these individuals cannot obtain sufficient food, they must emigrate or starve.

After constructing models of vertebrate populations composed of individuals with varying degrees of competitive ability, Sutherland and Parker (1985) argued that "the average individual in the population can be doing very well despite the population being at carrying capacity". They concluded that the proportion of time spent feeding at the population level is not a good measure of whether the population is limited by food supply and that it will probably be necessary to concentrate on the factors affecting the poorest feeders in the population to understand the carrying capacity and population dynamics of many vertebrates. In sea otters in California, the poorest feeders appear to be the juvenile females; also, many pups die before weaning (Chapter 2). In Alaska, some females apparently abandoned pups prior to the age of weaning (Garshelis and Garshelis, 1987). These authors hypothesized that the abandonment was related to the poor health of the female due to nutritional stress.

The exact mechanisms that are operating to slow the growth of the California sea otter population remain unclear. However, we believe that additional research on mortality factors in pups and independent juveniles, particularly juvenile females, would be likely to provide a better understanding of the dynamics of the California sea otter population.

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CHAPTER 5

FEEDING PATTERNS OF CALIFORNIA SEA OTTERS

K. RALLS, B. HATFIELD AND D. B. SINIFF

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INTRODUCTION

Because sea otters can often be easily observed from shore, their diet and foraging patterns have been studied in various parts of their range (Estes, Jameson, and Johnson, 1981; Ostfeld, 1982; Garshelis, 1983; Lyons, 1987). Most existing data have been obtained by visual observations of foraging otters. Relatively little is known about night-time foraging patterns, although studies using radio-telemetry have shown that sea otters in California do forage by night as well as by day (Loughlin, 1977; Ribic, 1982).

Early studies primarily yielded information about diet and foraging patterns at the population level. They showed that the California population feeds almost entirely on macroinvertebrates, although some populations in Alaska and the U.S.S.R. also feed on epibenthic fish, and that there appeared to be a great deal of variation in the diet and foraging patterns of individual otters (Estes, et al., 1981). Recently, studies on otters that could be individually identified by flipper-tags have confirmed that individuals tend to specialize on one to three or more of the many available types of prey and shown that these patterns of specialization may be maintained for three or more years (Lyons 1987).

Although we collected some data on uninstrumented otters, we focused on the foraging patterns of individual instrumented otters as indicated by radio-telemetry. Foraging sea otters alternatively dive to search for prey and return to the surface to breathe and consume their catch. Because radio signals are not transmitted through sea water, we could measure the length of dives and surface intervals whether or not we could see the instrumented otters. We present data on dive and surface intervals, the length of feeding bouts and the intervals between them, diurnal and nocturnal foraging patterns, and variation in foraging patterns within and between age/sex classes. We also compare data collected by listening to the radio signal with those collected visually and discuss the way in which variation in foraging patterns appears to be related to competition among individuals.

METHODS

The majority of data were collected during watches intended primarily to obtain information on time budgets and activity patterns (Chapter 4). Most of these watches were 24 to 48 hours in length. Shorter watches, designed specifically for the collection of feeding data, were conducted during morning and evening feeding periods on the otters in Morro Bay (otters 1-4). Data on the feeding activities of unidentified,

uninstrumented otters were also collected during one two-week period to obtain additional information on dive and surface interval lengths in relation to the size and type of captured prey.

The length of dives and surface intervals was measured from the radio signal from the instrumented animals and by visual observation of the uninstrumented otters. As visual observations indicated that the occasional dives shorter than 10 seconds were rarely feeding dives and that surface intervals shorter than five seconds were almost always the result of interruption by another otter, these were excluded from analyses. When possible, foraging individuals were observed from the shore through a high resolution telescope (Questar, 50x or 80x magnification), and the number, size, and species of captured prey were recorded.

Lengths of feeding bouts and the intervals between bouts were measured to the nearest minute. If more than 30 minutes elapsed between two feeding dives, these two dives were taken as the end of one feeding bout and the beginning of a second feeding bout, respectively. Records with a large amount of activity recorded as "unknown" and those where there was any ambiguity as to the end of a feeding bout were not used for the determination of bout and interval length. Only complete feeding bouts were used for the calculation of feeding bout length but intervals between bouts were measured as long as the ending of the first bout and the beginning of the next were known. We defined the day as the period from 1/2 hour before sunrise to 1/2 hour after sunset.

Otters were assigned to sex and age classes based on their weight at capture; estimated age, often based on the examination of cementum layers in a vestigial premolar extracted for this purpose; and, in the case of females, reproductive performance. All juveniles were judged to be no more than two years of age (Chapter 2).

Statistical comparisons among age and sex classes were performed using analysis of variance, controlling for variation among individuals within classes. We performed a log (base 2) transform on the data to reduce heterogeneity of variances. All statements that differences are statistically significant are based on the 0.05 probability level.

RESULTS

Observations from the shore

Because our instrumented otters often foraged at times when or in areas where they could not be easily observed, many of our visual observations were made on uninstrumented otters.

The data presented here consist of all visual observations on both instrumented and uninstrumented otters. The mean length of observed dives was 52.14 seconds (n = 712). Dive length varied with prey type to some extent, being least for mussels and greatest for octopus (Table 5.1) but was not related to prey size (Table 5.2). Surface times were clearly related to both prey type (Table 5.3) and prey size (Table 5.4). They were longest for large prey such as crabs, abalone, and octopus that often took an otter several minutes to eat.

Success rate varied with prey type. Otters foraging on mussels and small, hard-bodied prey that they pounded with a rock had the highest success rates while those foraging on large, calorically rich prey such as clams, abalone, and crabs of the genus Cancer had the lowest success rates. These relationships were evident even within age/sex classes for a sample of the instrumented animals (Table 5.5).

Data collected from the radio signal

The data presented here consist of dive lengths, surface intervals, feeding bout lengths, and the lengths of intervals between feeding bouts, all of which were collected from the instrumented otters regardless of whether or not the animals were seen.

Dive length -- The unweighted mean dive length for all instrumented otters was 73.56 seconds (n = 8254). Mean dive lengths for the individual instrumented otters ranged from 41 to 149 seconds (Table 5.6).

Analysis of variance on the log-transformed data indicated that there were significant differences among the lengths of the dives made by individuals within age/sex classes (Appendix 5.1). There were significant differences in dive length between age/sex classes (Table 5.7). Scheffe's test showed that adult males made shorter dives than adult females, who in turn made shorter dives than juvenile females and adult females with pups. Juvenile males made the longest dives, with a mean length of 116 seconds. The short dive times for adult males reflect the large proportion of dives from adult males in the relatively shallow waters of Morro Bay in our sample for this age/sex class.

The distributions of dive lengths for the different age/sex classes showed that adult males and adult females with pups had more individual variation in dive lengths than the members of the other age/sex groups (Fig. 5.1). The distribution of dive lengths for juvenile males indicates considerable internal consistency, even though the average dive length for this group was by far the longest (Fig. 5.1).

TABLE 5.1 - A comparison among the average dive lengths (sec) for sea otters prior to the capture of various types of prey in California.

PREY TYPE	DIVE LENGTH MEAN (SEC)	N	VARIANCE
MUSSEL	33.81	296	217.70
CRABS (All)	56.07	261	831.76
CRABS (Pugettia)	56.27	60	1186.86
CLAMS	58.09	220	517.94
CRABS (Cancer)	59.10	79	790.88
SEA STAR	64.65	23	1361.44
ABALONE	71.69	39	557.34
POUNDED WITH ROCK	78.66	196	1576.49
TUNICATE	79.18	28	230.29
OCTOPUS	101.71	28	2493.63

TABLE 5.2 - The average length of the feeding dives (sec) made by sea otters in California prior to the capture of prey of different sizes.

PREY SIZE	DIVE LENGTH MEAN (SEC)	N	VARIANCE
NONE	63.34	1149	741.06
SMALL	57.91	636	1245.61
MEDIUM	60.39	214	716.18
LARGE	64.90	229	882.29
EXTRA LARGE	61.37	147	674.06

Surface interval -- The unweighted mean surface interval for all otters was 64.50 seconds (n = 7944). Mean surface intervals for individual otters ranged from 25.5 to 155.3 seconds (Table 5.8). Analysis of variance on the log-transformed data indicated that there were significant differences among the lengths of surface intervals for the individuals in all age/sex classes except the juvenile males (Appendix 5.2). There were also significant differences among

TABLE 5.3 - A comparison among the lengths of the surface interval (sec) that were required to consume the various prey items taken by sea otters in California.

PREY TYPE	LENGTH OF SURFACE INTERVAL MEAN (SEC)	N	VARIANCE
TUNICATE	33.25	28	98.76
SEA STAR	54.00	23	675.65
MUSSEL	58.18	291	1290.32
CRABS (Pugettia)	94.22	55	6498.75
CLAMS	95.14	219	4398.47
POUNDED WITH ROCK	97.60	195	3860.78
CRABS (ALL)	120.67	267	19198.31
OCTOPUS	132.89	28	21610.38
ABALONE	150.92	39	25252.22
CRABS (Cancer)	213.39	85	34860.80

TABLE 5.4 - A comparison among the average lengths of the surface intervals (sec) that were required to consume various sizes of prey taken by sea otters in California.

PREY SIZE	LENGTH OF SURFACE INTERVAL MEAN (SEC)	N	VARIANCE
NONE	30.36	1095	1050.30
SMALL	55.56	635	2839.58
MEDIUM	62.34	216	2436.76
LARGE	122.59	226	14734.20
EXTRA LARGE	177.66	148	22886.74

the age/sex classes (Table 5.9). Adult females with pups tended to have the longest surface times, followed by juvenile males, and then a group consisting of the juvenile females, adult males, and adult females (Table 5.9). These trends were also apparent in the distributions of surface intervals for the age/sex classes (Fig. 5.2).

TABLE 5.5 - A comparison among the instrumented individuals in the various sex/age categories for the percentage of successful dives during feeding bouts. AF = adult female without pup; AFP = adult female with pup; AM = adult male; JF = juvenile female. No data were obtained for the juvenile males.

OTTER NUMBER	AGE/SEX CLASS	NUMBER SUCCESSFUL DIVES	NUMBER UNSUCCESSFUL DIVES	SUCCESS RATE (PERCENT)	PRINCIPAL PREY TYPE
15	AF	102	115	47	ABALONE/OTHER*
6	AF	173	59	75	CRABS
22	AF	41	2	95	SHB**
16	AFP	34	32	52	CRABS
25	AFP	109	5	96	MUSSELS
1	AM	244	616	28	CLAMS
3	AM	33	63	34	CLAMS
7	AM	47	12	80	CRABS
17	AM	82	15	85	CRABS[1] /SHB**
4	AM	162	18	90	MUSSELS
44	JF	31	40	47	CRABS#[2]
37	JF	25	24	51	CRABS
40	JF	44	27	62	CRABS
45	JF	31	15	67	CRABS[2]
46	JF	142	8	95	SHB** @

* -- Otters with two prey types listed caught approximately equal numbers of each type.
SHB** -- unidentified small, hard-bodied prey that were pounded with a rock.
-- Four of the prey items captured were stolen by other otters.
@ -- Three of the prey items captured were stolen by other otters.
[1] -- Pugettia
[2] -- Cancer

TABLE 5.6 - A comparison of the average dive lengths (sec) recorded for individual instrumented sea otters during feeding bouts. AF = adult female without pup; AFP = adult female with pup; JF = juvenile female; AM = adult male; JM = juvenile male.

OTTER NUMBER	AGE/ SEX	DIVE LENGTH MEAN (SEC)	N	VARIANCE
46	JF	41.48	427	485.47
4	AM	41.50	161	255.80
9	AF	45.66	772	323.87
15	AF	52.28	774	653.49
1	AM	57.05	733	647.24
37	JF	57.77	70	258.72
3	AM	58.03	88	650.03
34	AM	61.46	69	3694.60
16	AFP	61.73	194	487.53
16	AF	62.69	179	1224.25
25	AFP	66.91	487	1297.79
45	JF	71.52	406	689.53
39	JF	71.85	239	369.36
19	AF	73.94	48	330.10
2	AM	74.91	22	626.45
6	AF	76.89	1006	818.20
7	AM	77.48	101	1298.72
17	AM	80.13	210	3411.17
36	AFP	83.20	119	976.18
44	JF	83.52	326	540.65
42	JF	92.33	271	1062.93
40	JF	92.86	308	1129.69
13	JM	95.91	107	1861.67
43	JM	100.50	22	2245.70
27	AFP	100.56	179	1077.39
47	JF	104.93	160	2580.98
30	JM	115.64	119	1183.44
41	JM	132.43	127	231.01
29	JF	132.46	118	1409.91
35	JM	135.82	123	1717.04
22	AF	140.18	153	1019.31
14	AFP	149.40	136	1106.62

Feeding bouts -- Mean feeding bout lengths for individual otters ranged from 77 to 373 minutes (Table 5.10). The shortest mean bout length was for an adult male feeding primarily on clams in Morro Bay and the longest was for a juvenile female feeding on small, hard-bodied prey items in the Piedras Blancas area. Tallying the number of individuals within the age/sex classes according to the mean length of feeding bout suggested that juvenile females, and to a lesser

FIGURE 5.1 -- The distribution of dive times during feeding bouts for adult males, adult females, adult females with pups, juvenile females and juvenile males in California.

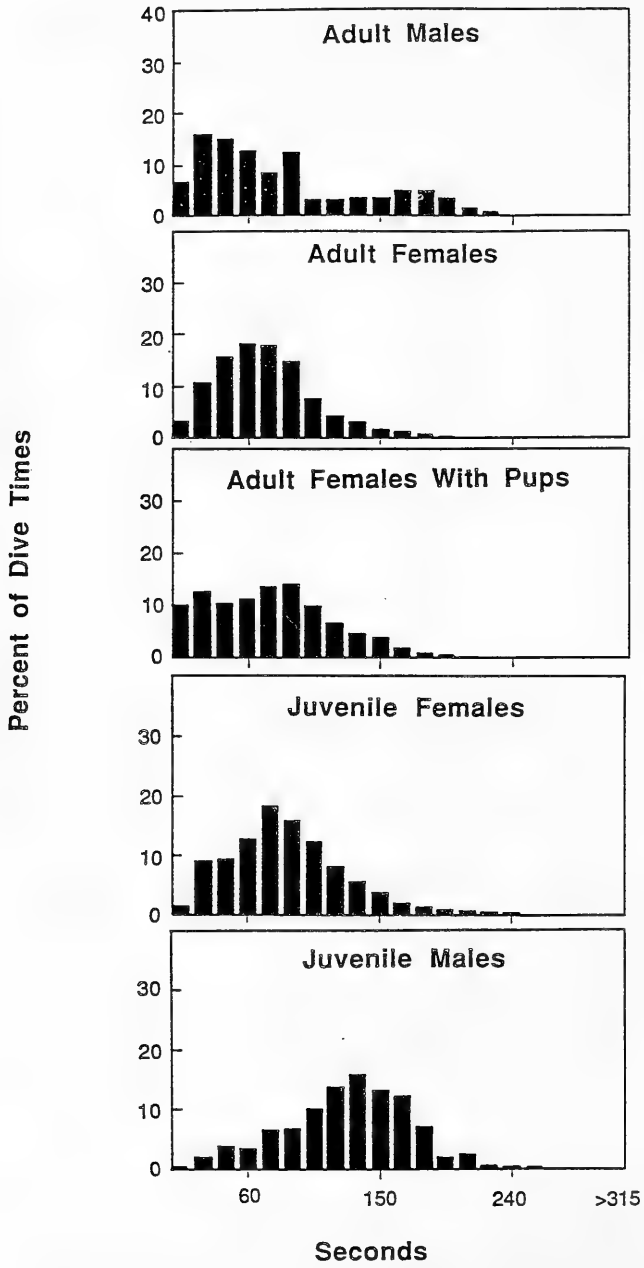

FIGURE 5.2 -- The distribution of the length of time of the surface intervals during feeding bouts for adult males, adult females, adult females with pups, juvenile females and juvenile males in California.

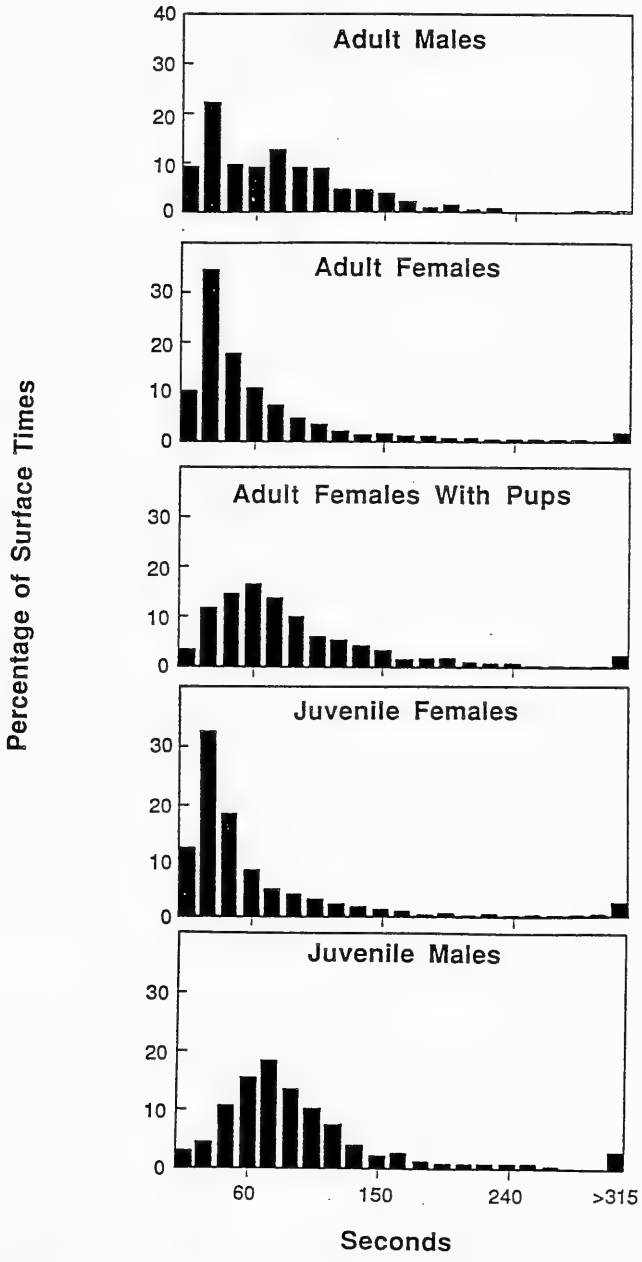

TABLE 5.7 -- Analysis of variance testing for differences in the length of the dives made by otters belonging to the various age/sex classes. Abbreviations as in Table 5.6.

Source	df	Mean square	F	p
Total	7937			
Among age/sex classes	4	128.37	242.2	<0.001
Error	7933	6.53		

Test of means:

	AM	AF	JF	AFP	JM
Mean dive length (sec)	64	75	83	92	116

The means for the age/sex classes underlined by the same line are not significantly different from each other (P<0.05, Scheffe's test).

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extent, adult females, tended to have long feeding bouts (Table 5.11A). The two individuals with mean feeding bout lengths over 250 minutes were both juvenile females (otters 45 and 46). When we tallied the number of bouts of various lengths for each age/sex class (Table 5.11B), we noted that juvenile females tended to be the most different from the others. Chi-square analysis testing for shifts in the distribution of lengths of feeding bouts among sex/age classes (Table 5.11B) showed a highly significant difference ($p<0.01$). When we eliminated the juvenile females from the analysis, the Chi-square was no longer significant, even at the 0.05 level, indicating no difference in bout length among the remaining age/sex classes.

Interval between feeding bouts -- The mean interval between feeding bouts was 187.7 minutes ($n = 228$). This is close to the approximately 180 minutes required for food to pass through the digestive system (Stulken and Kirkpatrick, 1955; Costa, 1982). Values for individuals ranged from 80.9 to 300.9 minutes (Table 5.12). Juvenile females and females with pups appeared to have shorter intervals between feeding bouts than the other age/sex classes. However, Chi-square analysis of the data in Table 5.13B indicated that there was not a significant difference among age/sex classes in the pattern of the distribution of lengths of the time between feeding bouts.

Comparison of day and night foraging patterns

We were able to compare day and night foraging patterns in four age/sex groups: adult females, adult females with pups, juveniles males and juvenile females. Unfortunately, we had insufficient data on the nocturnal foraging patterns of adult males to include them in this analysis.

TABLE 5.8 - The average surface times (sec) for individual instrumented sea otters that were recorded during feeding bouts. Abbreviations as in Table 5.6.

OTTER NUMBER	AGE/ SEX	SURFACE TIME MEAN (sec)	N	VARIANCE
37	JF	25.52	69	1137.81
46	JF	38.72	424	1835.33
19	AF	39.86	44	696.03
9	AF	43.43	744	1972.60
39	JF	44.19	242	1016.50
3	AM	49.23	86	4547.46
15	AF	49.43	732	4359.00
1	AM	50.17	701	3140.20
45	JF	50.56	396	7165.18
6	AF	52.14	985	3300.86
7	AM	52.52	99	3119.66
2	AM	53.40	20	1745.54
4	AM	59.99	158	2359.77
25	AFP	65.98	453	2467.77
44	JF	67.27	324	11250.17
42	JF	69.38	276	6846.35
40	JF	77.71	301	8128.68
16	AFP	78.22	188	6867.25
41	JM	84.26	125	293.02
35	JM	84.47	113	5525.51
17	AM	88.36	190	9636.31
34	AM	91.17	63	3750.24
47	JF	92.47	158	9386.40
27	AFP	93.54	163	10118.73
30	JM	94.43	115	6304.85
16	AF	96.74	170	16644.03
43	JM	102.29	21	7415.98
13	JM	106.17	103	9990.12
29	JF	106.93	109	6643.02
14	AFP	131.90	119	1697.86
36	AFP	139.50	105	10092.75
22	AF	155.33	148	7428.96

TABLE 5.9 - Analysis of variance testing for differences between the mean length of the surface intervals made by otters of the various age/sex classes. Abbreviations as in Table 5.6.

Source	df	Mean square	F	p
Total	7645	168.98	132.01	<0.001
Among age/sex classes	4			
Error	7641			

Test of means:

	JF	AM	AF	JM	AFP
Mean surface interval length (sec):	63	64	73	94	102

Dive length -- Analysis of variance of the log-transformed data indicated that there were significant differences between the length of day and night dives for the adult females with pups and the juvenile females but not for the adult females without pups and the juvenile males (Appendix 5.3). However, there were significant interactions between individuals and the length of day and night dives for all four age/sex groups.

The mean lengths of the day and night dives of the individual otters are compared in Table 5.14. Some individuals made longer dives at night, some during the day, and others made dives of about the same length during both periods. Only two of the four adult females with pups tended to make longer dives at night, even though the analysis of variance indicated a significant difference between day and night dive length for this group. The juvenile females tended to make longer dives during the day but again there was no consistency within the group (as indicated by the significant interaction terms in the ANOVA), with only four of the seven individuals making significantly longer dives during the day.

Surface intervals -- Analysis of variance of the log-transformed data indicated that there were significant differences between the length of the day and night surface intervals for the juvenile males and females but not for the adult females or the adult females with pups (Appendix 5.4). There were significant interactions between individuals and the length of day and night surface intervals for all age/sex classes except the adult females with pups. The mean lengths of the day and night surface intervals of the individual otters are compared in Table 5.15. The general pattern was similar to that for the dive length data in that some otters

TABLE 5.10 - The average lengths of the feeding bouts (min) that were recorded for individual instrumented sea otters. Abbreviations as in Table 5.6.

OTTER NUMBER	AGE/SEX CLASS	BOUT LENGTH MEAN (MIN)	N
1	AM	77.33	15
13	JM	88.00	5
36	AFP	90.00	9
41	JM	97.50	24
30	JM	99.50	8
27	AFP	103.90	10
9	AFP	106.60	5
11	AF	109.50	6
34	AM	111.57	7
29	JF	118.67	6
22	AF	119.23	13
16	AF	126.27	15
43	JF	130.40	10
14	AFP	133.60	5
35	JM	133.64	17
17	AM	134.63	11
16	AFP	138.29	7
7	AM	139.71	7
6	AF	142.66	18
43	JM	145.67	3
25	AFP	145.77	9
39	JF	146.50	9
19	AF	166.56	16
15	AF	171.06	16
42	JF	176.43	7
37	JF	186.60	5
40	JF	195.70	10
9	AF	201.25	4
36	AF	237.33	3
47	JF	244.42	7
45	JF	368.50	4
46	JF	373.00	3

TABLE 5.11 - The lengths of feeding bouts (min), grouped by time intervals, classified by the five age/sex categories of adult males, adult females, adult females with pups, juvenile females, and juvenile males. Part A is a tabulation of the average feeding bout lengths of each instrumented otter. Part B is a tabulation of the lengths of the individual feeding bouts.

A. MEAN FEEDING BOUT LENGTHS OF INDIVIDUAL OTTERS WITHIN CLASSES

BOUT LENGTH (MIN)	ADULT MALES	JUVENILE MALES	FEMALES WITH PUPS	ADULT FEMALES	JUVENILE FEMALES
<150	4	5	6	3	3
150-250	0	0	0	4	4
>250	0	0	0	0	2

B. LENGTH OF INDIVIDUAL FEEDING BOUTS WITHIN CLASSES

BOUT LENGTH (MIN)	ADULT MALES	JUVENILE MALES	FEMALES WITH PUPS	ADULT FEMALES	JUVENILE FEMALES
<150	19	41	30	40	29
150-250	6	14	13	23	14
>250	2	2	2	10	17

had longer surface intervals at night, some during the day, and others had surface intervals of about the same length during both periods. However, fewer otters (nine) had significant differences between the length of day and night surface intervals than between day and night dive lengths (15) and values of the test statistic, K, tended to be smaller for surface intervals for dive lengths.

Feeding bouts -- The mean length of entirely nocturnal feeding bouts (119.16 minutes, n = 43) was similar to that of those that occurred entirely during daylight hours (120.67 minutes, n = 62) but bouts that spanned the transition period from day to night or night to day tended to be considerably longer (209.80 minutes, n = 25).

DISCUSSION

Comparison of data with existing data sets

The results of our visual observations agree with those of the principal previous study in California (Estes, et al., 1981). Our overall mean dive time was 52 seconds; Estes, et

TABLE 5.12 - The average lengths of the intervals between feeding bouts (min) that were recorded for the individual instrumented sea otters. Abbreviations as in Table 5.6.

OTTER NUMBER	AGE/SEX CLASS	LENGTH OF INTERVAL BETWEEN BOUTS MEAN (MIN)	N
27	AFP	80.89	9
7	AM	96.67	3
14	AFP	103.60	5
37	JF	113.50	4
29	JF	121.60	5
41	JM	121.91	22
44	JF	122.89	9
25	AFP	139.77	9
39	JF	143.57	7
47	JF	146.57	7
9	AFP	160.20	5
36	AF	167.33	3
42	JF	170.00	5
35	JM	170.29	14
40	JF	175.38	8
45	JF	176.00	4
17	AM	177.78	9
16	AFP	179.17	6
36	AFP	184.00	6
6	AF	222.35	14
16	AF	233.54	11
13	JM	236.25	4
11	AF	242.80	5
9	AF	244.33	3
22	AF	254.50	12
30	JM	254.86	7
34	AM	272.60	5
19	AF	287.46	15
15	AF	300.91	12

TABLE 5.13 - The lengths of the intervals between feeding bouts (min), grouped by time intervals, classified by the five sex/age categories of adult males, adult females, adult females with pups, juvenile females, and juvenile males. Part A is a tabulation of the average interval between feeding bouts for each instrumented otter. Part B is a tabulation of the individual intervals between feeding bouts.

A. AVERAGE INTERVAL BETWEEN BOUTS FOR INDIVIDUAL OTTERS

INTERVAL LENGTH (MIN)	ADULT FEMALES	ADULT FEMALES WITH PUP	ADULT MALES	JUVENILE MALES	JUVENILE FEMALES
<150	0	3	1	1	6
150-250	4	3	2	2	3
250-350	3	0	1	2	0
350-450	0	0	0	0	0
450-550	0	0	0	0	0
>550	0	0	0	0	0

B. INDIVIDUAL BOUTS

INTERVAL LENGTH (MIN)	ADULT FEMALES	ADULT FEMALES WITH PUP	ADULT MALES	JUVENILE MALES	JUVENILE FEMALES
<150	19	25	7	30	35
150-250	16	10	6	7	7
250-350	8	3	9	4	1
350-450	7	0	0	5	4
450-550	8	0	1	2	3
>550	3	3	0	1	0

al. (1981) reported mean dive times of 50 to 60 seconds. Like Estes, et al., (1981), we also found no relationship between dive length and prey size and that dive length was not greatly affected by prey type, with the exception of dives for a few prey types such as mussels, which tended to be short, or octopus, which tended to be long. We found that surface times were longer for large, calorically rich prey items and that success rates were higher for small prey items such as mussels; again this agrees with previous studies in both California (Estes, et al., 1981) and Alaska (Garshelis, 1983).

Although Loughlin's (1977) mean dive length of 57 seconds based on telemetry data was similar to that derived from visual observations (Estes, et al., 1981), the relatively few individuals he studied appear to have foraged close to shore

TABLE 5.14 - A comparison of the mean lengths of dives made during the day and night by the individual instrumented otters in the various age/sex classes. The Kruskal-Wallis test was used to test for differences between day and night means, at the 0.05 probability level.

OTTER NUMBER	DAY MEAN	N	NIGHT MEAN	N	LONGER DIVES
Adult females					
15	62.8	433	47.8	285	day
9	45.1	736	56.4	36	night
6	71.3	538	83.3	468	night
22	141.2	62	139.5	91	ns
36	66.9	52	95.9	67	night
Adult females with pups					
25	53.9	334	95.3	153	night
16	63.1	286	59.1	87	ns
27	94.9	75	104.6	104	night
14	147.7	80	151.8	56	ns
Juvenile males					
13	105.7	72	75.8	35	day
30	114.7	68	116.9	51	ns
43	40.6	7	128.7	15	night
41	131.7	105	137.9	22	ns
35	129.3	91	154.3	32	night
Juvenile females					
45	72.9	272	68.7	134	day
39	71.7	97	72.8	141	ns
40	102.3	206	73.8	102	day
46	49.9	217	38.9	210	day
44	84.6	266	78.8	60	day
42	90.2	124	94.2	147	ns
47	94.0	116	133.9	44	night
Adult males					
17	62.5	161	138.2	49	night

TABLE 5.15 - A comparison of the mean lengths of surface intervals made during the day and night by the individual instrumented otters in the various age/sex classes. The Kruskal-Wallis test was used to test for differences between day and night means, at the 0.05 probability level.

OTTER NUMBER	DAY MEAN	N	NIGHT MEAN	N	LONGER SURFACE INTERVAL
Adult females					
15	48.6	406	52.9	273	night
9	43.3	709	46.6	35	ns
6	54.0	522	50.1	463	ns
22	160.9	62	151.3	86	ns
36	119.4	46	155.2	59	ns
Adult females with pups					
25	66.6	312	64.7	141	ns
16	86.2	273	89.6	85	ns
27	78.6	67	104.0	96	night
14	130.6	73	134.0	46	ns
Juvenile males					
13	132.0	70	51.4	33	day
30	81.4	66	111.9	49	night
43	112.8	6	98.1	15	ns
41	87.2	102	71.1	23	ns
35	93.9	83	53.8	30	day
Juvenile females					
45	49.2	266	53.3	130	ns
39	49.4	96	40.7	146	day
40	78.5	206	75.9	95	ns
46	47.4	213	30.0	211	day
44	69.6	271	55.4	53	ns
42	77.8	127	62.2	149	day
47	80.6	114	123.3	44	ns
Adult males					
17	71.5	147	145.7	43	night

in the Monterey area. Our more extensive telemetry data indicated that visual observations of otter foraging in California tend to underestimate mean dive lengths. As Garshelis (1983) found that dive length was correlated with water depth in Alaska, this is probably because feeding otters can only be observed easily when they are foraging close to shore in relatively shallow water. The mean dive length for our instrumented animals was about 13 seconds longer than our estimate based on visual observations of both instrumented and

uninstrumented otters. Although Estes, et al., (1981) reported, based on visual observations, that "dives longer than 125 seconds almost never occurred" in California, we found that five of 31 otters had mean dive lengths that exceeded 125 seconds and that twelve otters had maximum dive lengths of over 200 seconds. The longest dive we timed was 246 seconds; previous reports of maximum dive lengths are 200 and 275 seconds for California (Estes, et al., 1981 and Loughlin, 1979, respectively), and 205 seconds in Alaska (Garshelis, 1983).

Visual observations have given the impression that adults forage in deeper water than juveniles (Estes, et al., 1981). Although our otter with the shortest mean dive length was a juvenile female, another juvenile female had a mean dive length of 132 seconds. Furthermore, juvenile males spent much of their time far offshore beyond the kelp beds and tended to forage farther offshore, and hence probably in deeper water, than otters of other age/sex classes (see Chapter 3). Because our juvenile males tended to forage so far from shore, we were unable to observe them feeding, but the radio signal indicated that they tended to make longer dives than otters in the other age/sex classes, with a mean length of 116 seconds. The behavior of such juveniles is clearly not reflected in previous data sets on sea otter diet and feeding patterns.

Diurnal and nocturnal foraging patterns

Many individual otters displayed differences in diurnal and nocturnal dive length patterns that may reflect a tendency to specialize on different prey species, that may tend to occur at different mean depths, by day and night. However, there was no general tendency for longer dive lengths during either time period. Some of the many prey items available to the California population may be more vulnerable at night. For example, crabs belonging to the genus Cancer and octopuses are generally thought to be nocturnal (Estes, et al., 1985; Ricketts, et al., 1986; Barr and Barr, 1983). Individual otters also vary in the extent to which they tend to feed at night. Since the mean length of diurnal and nocturnal feeding bouts was similar, differences in the distributions of diurnal and nocturnal surface intervals were less frequent than those for dive lengths, and the length of surface intervals is related to the size of prey consumed, most individuals may have similar diurnal and nocturnal rates of caloric intake.

Our data on the length of surface intervals were generally similar to those in other studies, in that the length of surface intervals increased with the size of the captured prey. However, the time required to consume captured prey is not the only factor affecting the length of surface intervals. Adult females with pups and juvenile males had the

longest surface intervals. Visual observations showed that these were, in part, the result of social interactions of the adult females with pups and of the juvenile males with other juvenile males.

Individual variation in foraging patterns

The degree of individual difference in foraging patterns among California sea otters is striking. Data presented in this chapter indicate that individuals vary with respect to the size and species of prey consumed, dive length, surface interval length, feeding bout length, and the degree of difference between diurnal and nocturnal feeding patterns. Data presented in Chapter 4 indicated that individuals also vary in the total amount of time spent feeding per 24-hr day and the proportion of time they forage at night.

Taken as a whole, these individual differences suggest that prey items are not equally available to all individuals in the California population. Juvenile females appear to be at a disadvantage compared to adults. They tended to feed for long periods and for a higher proportion of time than the other age/sex classes (Chapter 4). Much of their prey consisted of items that were too small to be identified and when they were successful in capturing a large, desirable prey item such as a crab belonging to the genus Cancer, this was often stolen by another otter. They often fed during the day when most otters were resting (Chapter 4), which probably helped them avoid competition with older animals.

Juvenile males often fed farther off-shore than the other age/sex groups (Chapter 3), on unknown prey species. As a group, juvenile males had longer surface intervals than juvenile females and their feeding bout lengths were similar to those of adults. In general, our results on foraging, time budgets and activity, movements, and survival strongly suggest that juvenile females tend to be at a disadvantage in the portion of the range where we studied.

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CHAPTER 6

AGE DETERMINATION OF CALIFORNIA SEA OTTERS FROM TEETH

P. PIETZ, K. RALLS, AND L. FERM

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INTRODUCTION

Determining the age of individuals by counting incremental lines in tooth cementum has proved to be a useful tool for a wide variety of mammal species (for a review see Grue and Jensen 1979). It has been used to estimate ages of both salvaged and living sea otters in Alaska (Schneider 1973 and Garshelis 1984, respectively).

Accurate age estimates of living animals offer potential insights into many aspects of sea otter biology, such as the age of first reproduction in females, the ages of territorial males, and age-related differences in movement patterns. Accurate age estimates of salvaged animals may also be useful as a means of estimating population age structure and, thus, for constructing models that can detect and predict changes in population parameters.

METHODS

In an effort to gain insight into the age structure of the California population, we have studied a sample of premolars from more than 580 sea otters. We extracted 30 premolars (PM_1, as recommended by Schneider 1973) from animals that were captured and radio-tagged; we collected the rest from skulls of dead otters salvaged by the California Department of Fish and Game and the U.S. Fish and Wildlife Service. Skulls of many salvaged animals had been deposited at numerous institutions and agencies. The majority of our teeth were taken from skulls in collections at the following institutions: Santa Barbara Museum of Natural History, California Polytechnic State University (San Luis Obispo), California Department of Fish and Game (Monterey, Morro Bay), U.S. Fish and Wildlife Service (Piedras Blancas), University of Puget Sound, and San Jose State University.

The teeth were decalcified, sectioned, and stained by Gary Matson, P.O. Box 308, Milltown, Montana. From teeth mounted in paraffin, he cut longitudinal sections 14 m thick and stained them with Wolbach's Giemsa. Basic procedures (Luna 1968) were modified in conjunction with advice from Aleta Hahn of the National Marine Fisheries Service (S.W. Fisheries Center, P.O. Box 271, La Jolla, California). To determine ages, we counted bands in the cementum of the sectioned teeth using criteria outlined by Schneider (1973) for Alaskan otters.

RESULTS AND DISCUSSION

Despite the extensive analyses of sea otter teeth conducted by Schneider (1973) and Garshelis (1984), there are presently only a few teeth available from known-age otters.

This makes it difficult to evaluate the relationship between cementum lines and annual time intervals with certainty. However, we have been able to examine teeth from ten California otters of known minimum age, and the age estimates from these teeth compare quite favorably with the age estimates of the otters made by field biologists (Table 6.1). Comparisons of ages determined from tooth cementum with known ages for animals of a variety of other species are shown in Table 6.2. Although there is exact agreement in most cases, there is a difference of more than one year in a few

TABLE 6.1 . Tooth age estimates for sea otters of minimum known age.

Univ. Minn. no.	FWS[a] no.	CDF&G no.	Sex	Date tagged	Est. age when tagged[b]	Date found dead	Est. age at death[b]	Tooth age
42	116	1142	F	10-82	1 - 2	1-83	1 - 2	1+
65	074	1012	F	10-80	0.5 - 1	9-81	1.5 - 2	2
68	115	1182	F	10-82	0.5 - 2	5-83	1 - 2.5	2
617	097	1106	M	10-81	0.5 - 1	8-82	1.5 - 2	2
41	-	1577	M	12-85	0.5 - 1	4-87	2 - 2.5	3
47	090	1170	M	10-81	0.5 - 2	4-83	2 - 3.5	4
616	-	1573	M	6-82	< 0.5	3-87	5	5
55	051	1269	F	7-79	4+	1-84	8.5+	6
440	-	715	F	12-72	1+	8-79	7.5+	8
615	-	1494	F	10-79	3+	5-86	9.5+	11

[a] All animals with FWS numbers were initially tagged by FWS. The others were tagged by CDF&G.

[b] Ranges include estimates by R. Jameson and J. Bodkin of FWS, to the nearest half-year.

cases. Judging by the data in Tables 6.1 and 6.2, the accuracy of the technique for sea otters may be similar to that for other species.

Our optimism regarding the value of the cementum technique for age determination for sea otters arises from three sources: (1) the correlation between cementum lines and yearly intervals in known-age animals of numerous other species (Grue and Jensen 1973, Grue and King 1984); (2) the correlation between cementum lines and age estimates made by field biologists in our ten sea otter teeth of "known"-age (Table 6.1); and (3) the correlation between age class assignments determined from sea otter skulls and from teeth (Fig. 6.1).

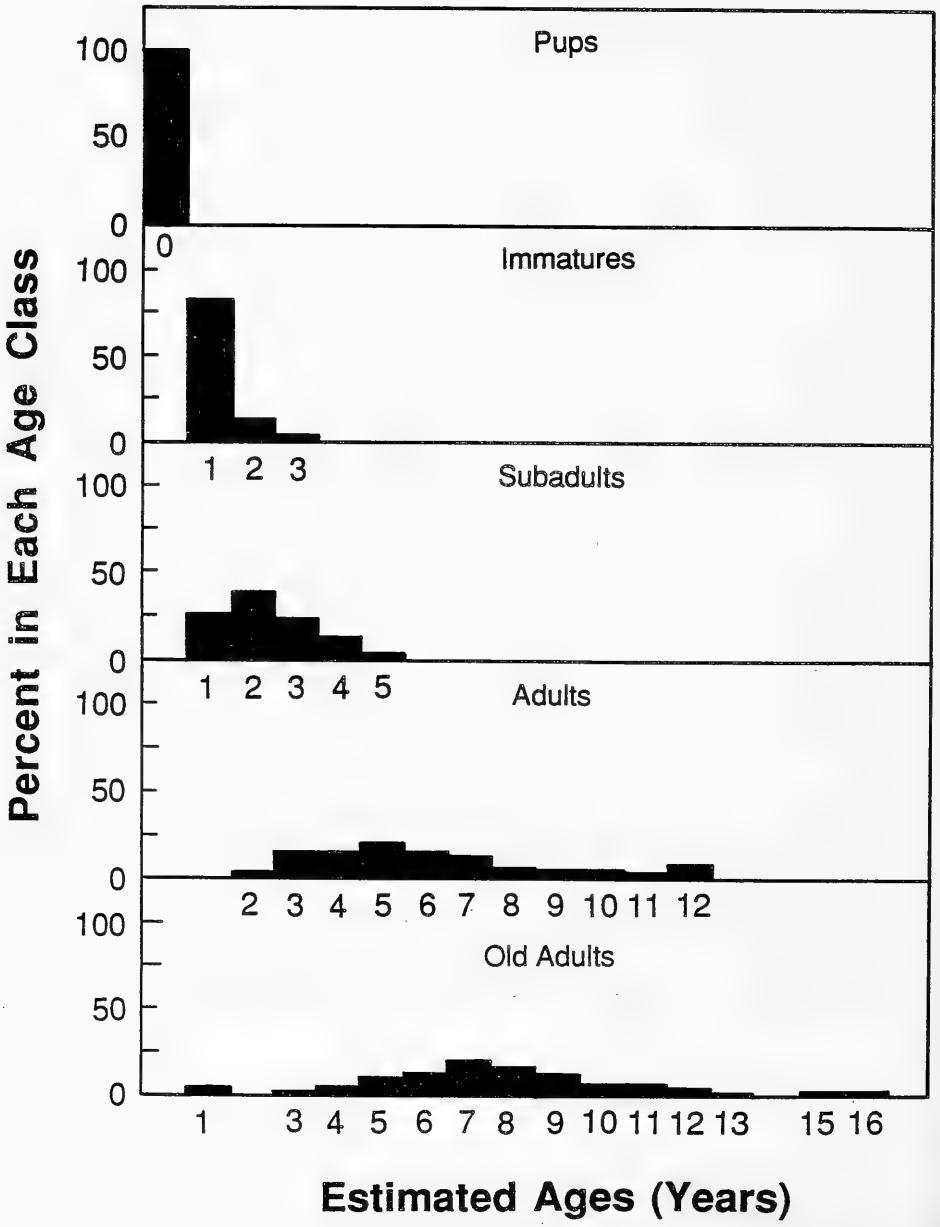
Age estimates based on skull features (e.g. suture closure, ridge development, tooth wear) were available for over 200 of the animals for which we have sectioned teeth. These estimates were provided by Jack Ames of the California Department of Fish and Game. He assigned skulls to five age categories: pups ($\leq$ 6 months old); immatures (probably about 1/2 to 1 1/2 years); subadults (probably 1-4 years); adults (probably at least 4 years), and old adults (probably at least 10 years). Comparing tooth age estimates from our most experienced reader to these categories, we found that 96-100% of our readings for animals in the "pup", "immature", and "subadult" categories fell within the appropriate age ranges (Fig. 6.1). As expected for the broader and less well defined categories of "adult" and "old adult", the range of tooth ages within each category was greater and the overlap between categories was greater. Nevertheless, 72% of teeth from animals in the "adult" category were assigned ages from 4-10 years and 71% of those in the "old adult" category, ages from 7-16 years.

Ages of teeth from older animals are the most difficult to assess. Garshelis (1984) noted that it was difficult to determine exact ages when more than about 10 cementum annuli were present because annuli were spaced so closely together in older animals. Teeth obtained from skulls stored in museums may offer an additional problem; according to Schneider (1973), teeth allowed to air-dry developed dark edges which made it difficult to differentiate outer annuli.

Despite these potential difficulties, our age assignments for teeth from "old adult" skulls were not unreasonably low. Male and female sea otters in Alaska have been estimated to live 10-15 and 15-20 years, respectively (Calkins and Schneider 1984). In California, the oldest tagged otters under observation are a 13-14 year-old female and two $\geq$ 12 year-old males (M. Riedman and J. Estes, pers. comm.). In our sample of 580 animals, the oldest age estimates based on tooth cementum were 16 years for two females and 15 years for two males.

The technique of determining age by counting cementum lines can best be evaluated with an extensive reference collection of teeth from known-age sea otters. We are now in the process of developing a reference collection, but this requires long-term effort and inter-agency cooperation. In the meantime, we have attempted to evaluate other aspects of the technique: (1) variation within and among readers, (2) variation among premolars of the same individual, and (3) variation in readability due to different methods of preparing skulls and teeth.

FIGURE 6.1 -- Comparison of age estimates based on teeth to age-class assignments for the same sample of otters made by the California Department of Fish and Game using skull features.



A total of 614 teeth were sectioned, stained, and "read" by at least one reader. A sub-sample of nearly 200 teeth was examined once by two readers and twice by one reader. About 100 of these teeth were examined once by four readers. Statistical analysis of the sub-sample of 100 showed no significant differences among the age distributions determined by three of the four readers or between readings made by the same reader. In two trials by the same reader, exact agreement between age assignments occurred in over 77% of 177 teeth. This reader showed a 0-1 year difference between age assignments for 98% of the teeth. None of this reader's age assignments were more than two years apart for a given tooth. Age assignments made by two different readers showed exact agreement for 52% of 179 teeth, a 0-1 year difference for 87%, and $\leq$ 2 year differences for 96% of the teeth. Age assignments among three readers showed a 0-1 year difference for 73% of 85 teeth, and $\leq$ 2 year differences for over 93% of these teeth. Table 6.3 gives more detailed results of comparisons between and within readers.

Multiple teeth from about 40 otters were sectioned, stained, and read by four readers in order to help us evaluate variability among teeth of individual otters. All four first premolars were available for 14 otters (boiled and broken teeth were excluded). Comparing ages assigned by individual readers with the modal age (across readers and teeth) for an individual otter, we found that over 67% of the assigned ages for 406 teeth were exactly the same as the mode, over 90% were 0-1 year away from the mode, and 96% were $\leq$ 2 years away from the mode (Table 6.3). These results compare well with age estimates of duplicate teeth from other species (Table 6.2).

Boiling skulls to facilitate cleaning has been a standard practice in many museums and laboratories. Schneider (1973), however, noted that extensive boiling of teeth made cementum lines less distinct. We compared the definition or distinctness of lines noted for boiled and unboiled teeth in our sample. Among the 516 teeth for which treatment during preparation was known, there were 60 teeth for which the reader noted "indistinct lines" or "poor definition." Half of these 60 teeth had been boiled, whereas only 34% of the other 456 teeth had been boiled. This difference was statistically significant ($Chi^2 = 5.775$, $df = 1$, $P < 0.025$), thus agreeing with Schneider's findings. We also examined pairs of teeth from individual otters that were purposely processed in different ways; i.e., of two teeth taken from the same animal, one was boiled and the other was not. Tooth sections were rated within pairs on quality of cementum line definition. For the six pairs available, the boiled tooth was always rated as poorer quality than the unboiled tooth (sign test, $P = 0.03$). We concur with Schneider in recom-

TABLE 6.2 -- A comparison of animal ages determined from tooth cementum by Gary Matson: (1) with animals of known age; (2) with duplicate determinations based on a different tooth from the same animal; and (3) with ages estimated from the degree of tooth wear (reprinted from Matson's Tooth Cementum Age Analysis, Progress Report No. 9, Spring 1987, Table 1).

Period	Kind of Comparison	Species	Number In Sample	Exact Agreement [a]	1 Year Difference	More than 1 Year Difference	Average Age
1978-82	Known Age	Various	28	22	4	2	5.0
1983-85	Known Age	Various	14	8	5	1	5.4 CA [b] 5.4 KA
1986	Known Age	BT Deer	1	1	0	0	4.5 CA 4.5 KA
1986	Known Age	WT Deer	25	22	1	2	3.3 CA 3.5 KA
1986	Known Age	Caribou	14	12	1	0	2.9 CA 2.9 KA
1986	Known Age	Kit Fox	9	7	2	0	2.1 CA 2.1 KA
1986	Known Age	B.H. Sheep	2	0	2	0	8.5 CA 9.5 KA
1986	Known Age	R. Otter	1	1	0	0	0.5 CA 0.5 KA
1986	Known Age	Raccoon	19	14	5	0	2.1 CA 1.9 KA
1984-85	Duplicate [c]	Elk, Coyote, Bobcat	112	89	21	2	2.9 [d] 2.7
1986	Duplicate	Bobcat	100	93	7	0	2.5 2.6
1986	Duplicate	Black Bear	138	91	34	13	5.2 5.2
1986	Duplicate	Pronghorn	10	8	2	0	5.2 5.0
1983-86	Duplicate [e]	Elk	1,915	1,730	152	33	5.8 5.8
1986	Duplicate [f]	Elk	88	45	36	7	4.9 5.0
1986	Comparison with wear	M. Deer	192	123	58	10	3.3 CA 3.5 WA [g]

a. Matson's age compared with age from a second source.
b. CA = Cementum age; KA = Known age.
c. A "duplicate" age determination was the analysis of 2 teeth from the same individual mammal without Matson's knowledge of the identity of the duplicates.
d. The first number given is the average age according to the first analysis, and the second number is according to the second analysis.
e. Two primary incisors were aged together to obtain greatest accuracy for each elk. Matson's knew of the duplication while aging, and the table shows the number and size of changes made when the ages of paired incisors differed.
f. Upper canine teeth. Sample collected and cementum aged over a period of several years and aged again in 1986.
g. WA = Aged by tooth wear and replacement.

mending that boiling be avoided in future specimen preparation.

TABLE 6.3 -- Comparisons of sea otter age assignments based on counts of incremental lines in tooth cementum.

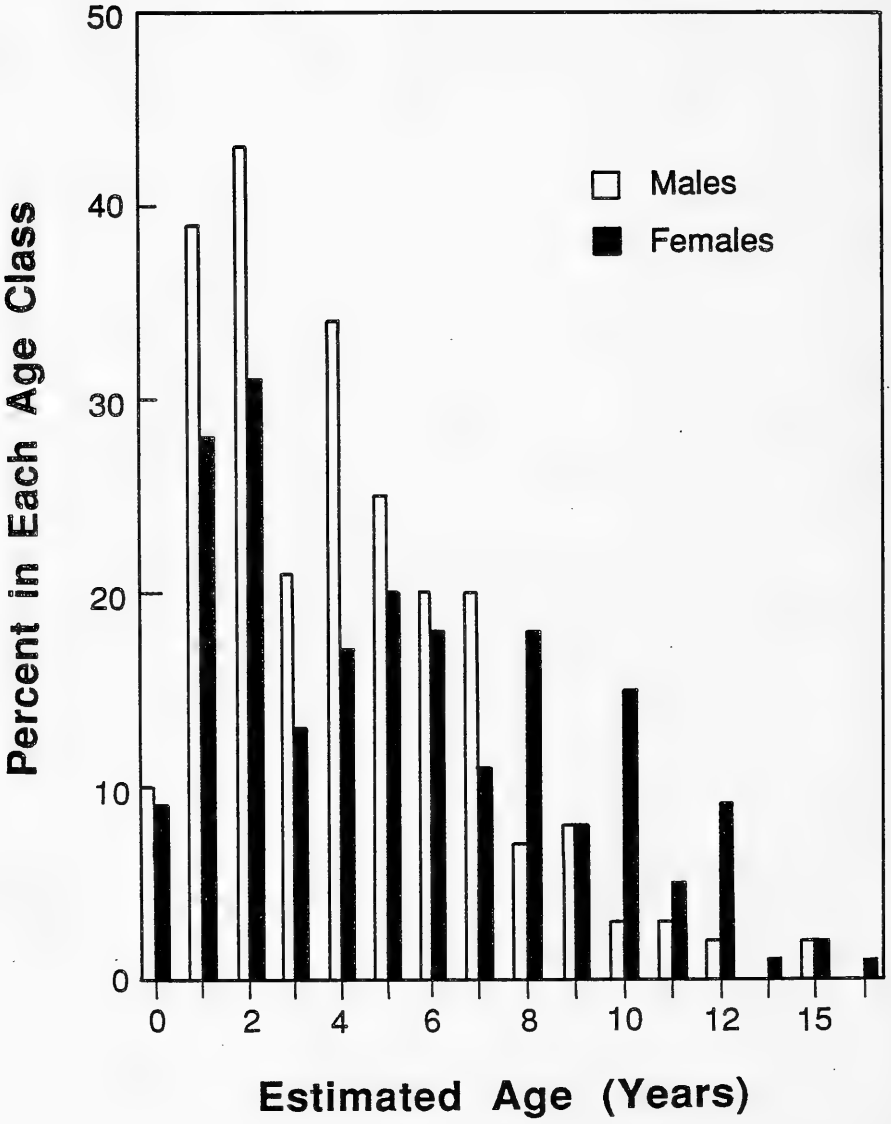
Age assignments compared between/among:	No. of teeth in sample [a]	Age assignments: no diff.	1-yr diff.	2-yr diff.	≥3-yr diff.
Trials A and B by reader 2	177	137	36	4	0
Readers 1 and 2A	179	93	62	16	8
Readers 1, 2A, and 3	85	37	25	17	6
Readers 1, 2A, 3, and 4	85	16	29	14	26
Teeth from the same otter	406	274	93	23	16

[a] No boiled teeth were included in these comparisons.

Finally, we evaluated the effects of air drying teeth on our ability to read outer annuli. For a group of otters from the same skull age category ("old adult"), we compared the average ages assigned to teeth collected "fresh" and stored frozen until slide preparation and teeth collected from museum specimens that were stored dry at room temperature. We found no statistically significant difference between the age distributions of these two groups ($Chi^2 = 3.04$, $df = 3$, $P > 0.25$). Our sample size was small (47 teeth), however, and thus should not be considered an endorsement for dry shelf storage of teeth.

We believe that counting cementum lines in teeth is a useful technique for determining ages of sea otters. We used tooth ages assigned by our most experienced reader for the age estimates of radio-tagged otters in California given in Chapter 2 and to obtain the age distributions of males and females, based on 425 teeth from dead animals of known sex in Fig 6.2.

FIGURE 6.2 -- Distribution of age estimates for 425 dead sea otters, based on incremental lines in tooth cementum.



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CHAPTER 7

ANALYSIS OF THE PRECISION AND ACCURACY OF RADIOTELEMETRY EQUIPMENT AND METHODS USED IN CALIFORNIA

A. MERCURE

NOVEMBER 30, 1988

INTRODUCTION

The positions of the sea otters, instrumented with radio transmitters, off the California coast in this study were estimated, when possible, by triangulating on the radio signals. The accuracy and precision of this method were studied by placing a radio transmitter on a buoy, establishing the location of the buoy by visual methods, and taking a series of compass bearings on the buoy's radio signal. In this chapter, I consider the field techniques associated with the estimation of the precision and accuracy of the triangulation measurements on these buoys, and provide quantitative estimates of error for otter-location data collected by field personnel.

METHODS

General procedures

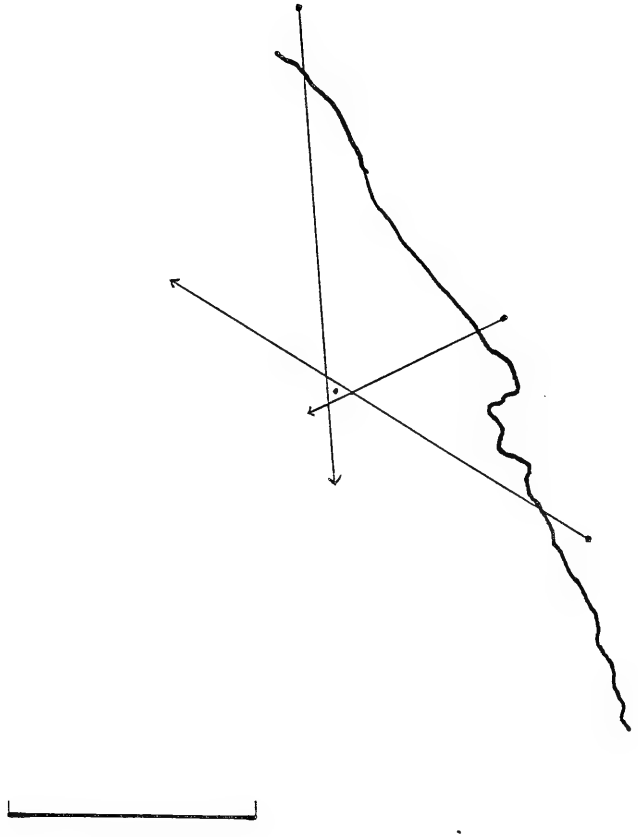
Radio transmitters were placed inside a styrofoam buoy to simulate a resting sea otter and the buoy was anchored off the California coast in two locations (south and north locations) near Piedras Blancas.

One of the first necessities of this work was to determine the map location of the two buoy locations. Both the south and the north buoy locations were determined by sighting through a Questar telescope from three positions along the shore. The coordinates of the three shore positions were obtained from our UTM grid on topographic maps of the study area. Compass bearings to the buoy were obtained by holding a Silva ranger compass against the Questar and reading the magnetic bearing from the compass. These bearings, along with the map coordinates of the three positions from which they were taken, were then used to plot the map location of the buoy. This method is illustrated in Fig. 7.1.

The accuracy of this method was initially tested by sighting on a prominent landmark (Piedras Blancas Lighthouse) and recording 12 compass bearings from the Questar to the landmark. Subsequently, the UTM topographic map coordinates of the Questar position and the landmark location (in UTM coordinates) were obtained and the true bearing between the two locations was determined from these coordinates. This bearing was then compared to the mean of the 12 Questar bearings.

Our normal field procedure when locating otters was to hold the compass by hand when taking bearings, rather than holding it against the Questar scope. To determine any additional variance that may have been contributed by holding

FIGURE 7.1 -- Illustration of the method used to determine the location of the buoy by taking compass bearings, from three locations along the California coast, to the signal from the radio transmitter on the buoy.



the compass by hand, an additional 25 bearings to the Piedras Blancas Lighthouse were taken using this method.

To check for possible effects of tides on the location of the buoys, we collected data on the location of the south buoy over several tidal cycles. One hundred twenty-one compass bearings using the Questar scope were taken from one position over a period of 300 hours.

Once the locations of the buoys had been determined in UTM coordinates, our next task was to use these known locations of the buoys to measure our ability to record accurate locations of sea otters. To do this, we used the same techniques and equipment we normally used to record bearings on the instrumented otters to record bearings on these buoys. The telemetry equipment consisted of two Ford vans with directional four-element yagi antennas and Cedar Creek Bioelectronics Laboratory radio receivers. The antenna was pointed towards the direction of the strongest radio signal, usually taken as mid-way between the two points at which the signal disappeared ("nulls"), and a compass bearing of this direction was determined by sighting along the antenna with the hand-held compass. Four different observers helped collect bearings toward the stationary buoys. Observers took bearings in blocks of 50. In order to disrupt the tendency to mechanically repeat prior readings, the mobile receiving unit was moved about one meter after every two readings and was completely turned around after every 10 readings. Bearings were taken from three different positions along the shore to the south buoy location and from two positions to the north buoy location.

The shore positions used for the south buoy location were similar to those used for the collection of actual sea otter location data, in that the angles of the intersections of the bearings from these positions were generally 90 degrees or less. However, the two shore positions used for the north buoy location were chosen to test for effects of signal bounce and estimate the extent to which error was related to the distance of the shore position from the transmitter. Here, bearing measurements were taken from positions four and six kilometers from the buoy and the angle between the bearings taken from these two positions was almost 180 degrees.

Establishing measures of precision and accuracy

Several methods have been developed to estimate the accuracy and precision of radio signal locations determined from bearing data. Lenth (1981) described three methods for estimating the location of a radio signal from the intersection of three bearings: the maximum likelihood estimator, the Huber estimator and the Andrews estimator. All

three are based upon probability distributions. The Huber and Andrews estimators are designed to be relatively insensitive to outlying points. Precision is defined by Lenth (1981) on the basis of an iterative algorithm and a variance co-variance matrix. Computer program TRIANG (Garrott, et al., 1986) calculates these estimators and defines the area of a 95% confidence ellipse around them, using the methods described by Lenth. Detailed mathematical descriptions are presented in Lenth (1981). Garrott, et al., (1986) also did an empirical test of the three estimators and found the Andrews estimator to be superior to the other two estimators. Confidence ellipses generated from the Andrews estimator were more likely to include the actual transmitter location and were found to be more accurate, i.e., the plotted point was usually closer to the actual transmitter location.

Our work with the buoys gave me a sample of bearings on a known location from several positions along the coast. These bearings did not correspond exactly to those used to locate otters, since they were repeated bearing measures on a known location. To more closely simulate field data, I took random samples of these bearings and used them to represent bearings that would have been recorded during field operations, if the buoy had been a resting sea otter.

One hundred bearings from each of the three shore positions for the south buoy were randomly chosen and one bearing from each position was randomly chosen and combined into a set of three. These 100 sets of three bearings were then used to triangulate the location of the transmitter and estimate precision and accuracy for the south buoy location.

The angle generated from bearings taken from the two shore positions for the north buoy approached 180 degrees, thus these data could not be used, as recorded, to estimate precision and accuracy. However, I was able to use the distribution of errors (degrees difference from the actual bearing) of the bearings taken on the north buoy. These error measures were placed in a random order and 50 sets of three were randomly drawn. Three positions along the California coast near the north buoy location were then selected so that the distance between them represented the maximum distance between the positions normally used when locating otters. The actual bearings from these positions to the north buoy were calculated from our topographic maps and the sets of errors were then added to the actual bearings to simulate field data.

Precision was defined as the 95% confidence ellipse, and accuracy was estimated by calculating the distance from the plotted point to the actual transmitter location. Calculations were made using the Andrews estimator and computer program TRIANG (Garrott, et al., 1986).

Comparisons of methods for estimating location from bearings

After the bearing data to the two buoy locations were generated, it was then necessary to compare the location estimates produced by our field method of plotting data and the Andrews estimator. Our field method consisted of plotting at least two, but preferably three, bearings to an otter on the topographic maps and then assigning a position in UTM coordinates to the point at the intersection of two bearings or in the center of the triangle formed by three bearings. To compare this method with the Andrews estimator, the 100 sets of bearings toward the south buoy and the 50 sets of simulated bearings toward the north buoy were plotted by the field method. The resulting location estimates and the Andrews estimators for the same sets of bearings were then compared to the actual buoy locations.

A direct comparison of the individual location estimates produced by the field method and the Andrews estimator was made using 50 otter locations, randomly chosen from our otter position data plotted in the field. These locations were recalculated by entering the bearings obtained in the field into a computer and again using program TRIANG to obtain the Andrews estimator.

RESULTS

Accuracy of determining buoy locations visually

The difference between the mean of the bearings to the lighthouse taken with the compass held against the Questar and the calculated true bearing was 0.6 degrees, with a standard deviation of 0.4 degrees. The difference between the mean of the hand-held compass bearings toward the lighthouse and the calculated true bearings was 1.6 degrees, with a standard deviation of 1.2 degrees. These data are summarized in Figures 7.2 and 7.3. It was not possible to read the compass to an accuracy greater than one degree.

The bearings taken to evaluate the possible effects of buoy movement due to changing tides are plotted against time in Fig. 7.4. No movements of the buoy over time were apparent.

Accuracy of bearings towards the radio signal from the buoys

The difference between the mean of the 897 hand-held compass bearings to the radio signals on the buoys and the calculated true bearing was 0.5 degrees (Table 7.1). The bearing error did not differ significantly with buoy location, shore position, van, or observer (Table 7.1). The

distribution of the differences between these bearings taken by field personnel and the calculated true bearings is shown in Fig. 7.5.

Precision and accuracy of triangulations on buoys

Table 7.2 summarizes calculations of the precision and accuracy of our simulated locations of the north and south buoys through radiotelemetry. Precision, defined as the 95% confidence ellipse, was estimated as between 0.03 and 0.08 hectares. The mean accuracies of our estimations of the locations of the buoy were 51 meters for the south location and 110 meters for the north location.

Comparison of field-method estimates with Andrews estimator

The results obtained by hand-plotting the 100 sets of bearings to the south buoy and the 50 sets of bearings to the north buoy and the Andrews estimator for these same data sets are compared in Table 7.3. Although the two methods gave similar results, in that, on the average, the estimated locations were about equally close to the true location of the radio signal, the actual data points calculated by the two methods were different. The mean difference between the 50 field data points and the Andrews estimator for the same bearings was 162 meters with a standard deviation of 104 meters. The reason for this difference is that the two procedures use different methods of weighting the bearings. The Andrews estimator is designed to be robust to outliers and thus assigns different weightings to individual bearings based upon a probability distribution. However, field personnel usually plotted the location of the otter in the middle of the triangle formed by the three bearings and thus gave equal weight to each of three bearings.

DISCUSSION

Errors in determining the true locations of the buoy by visual sightings with the Questar were minimal and appeared to be the result of our inability to read the compass to an accuracy of less than one degree and/or the limitations of our ability to locate points precisely on the topographic maps. The positions of the buoys did not change with the changing tides.

The accuracy of our bearings compared quite favorably with that of those taken in other radiotelemetry studies. Several studies have reported mean errors and standard

FIGURE 7.2 -- Distribution of 12 compass bearings to a prominent landmark sighted through a telescope (Questar). The actual bearing of the landmark (zero degrees in the figure) was calculated from the positions of the telescope and the landmark on a topographic map.

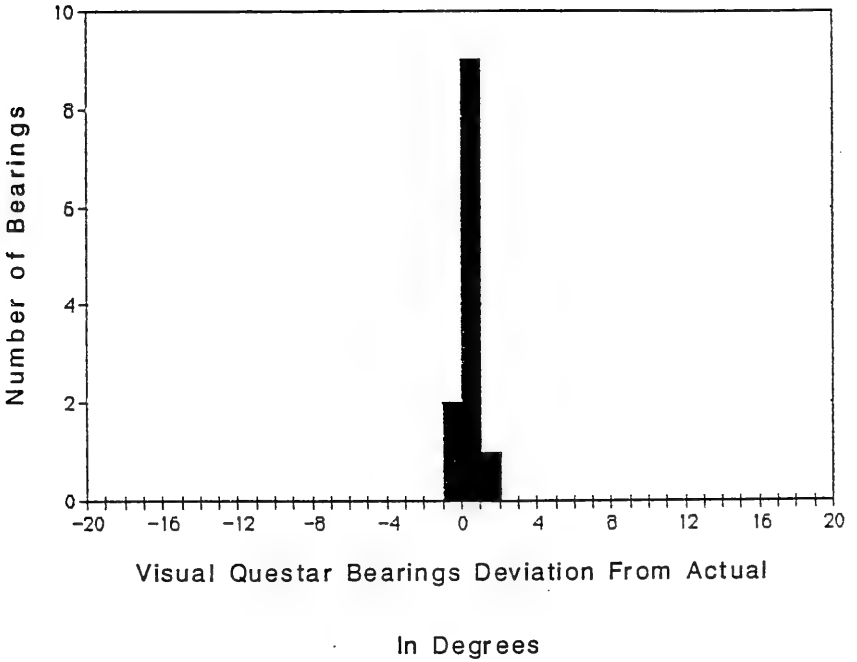


FIGURE 7.3 -- Distribution of 25 hand-held compass bearings to a prominent landmark. The actual bearing to the landmark was calculated as in Figure 7.1.

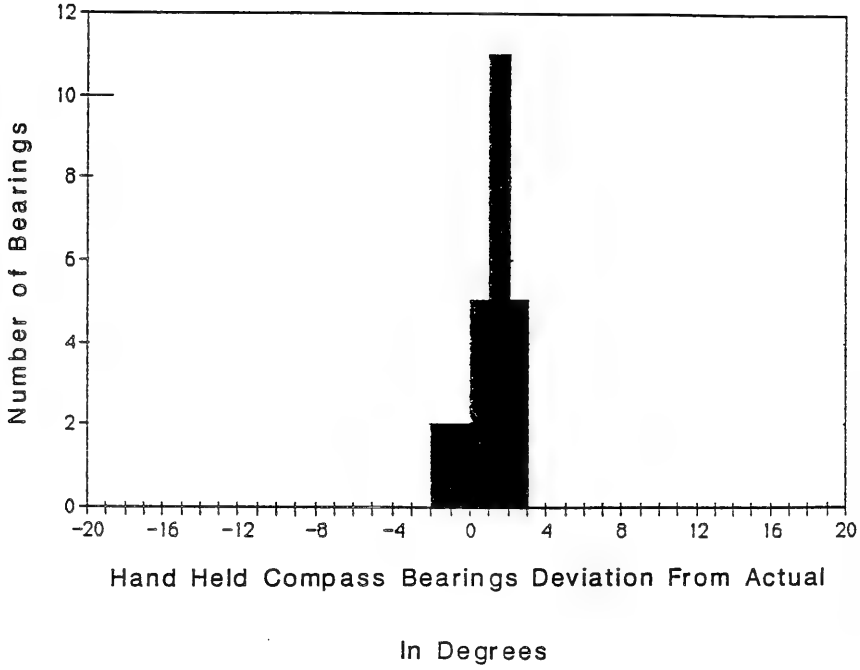


FIGURE 7.4 -- Compass bearings to a radio transmitter on a buoy off the California coast, taken over a three-hour period when the tide was changing.

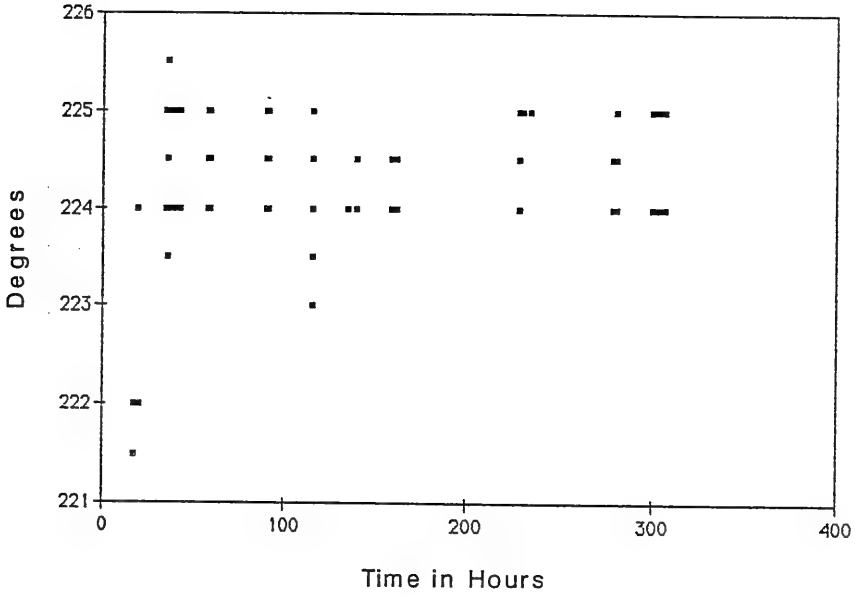


FIGURE 7.5 -- Distribution of 1125 hand-held compass bearings to the signals from radio transmitters on buoys off the California coast.

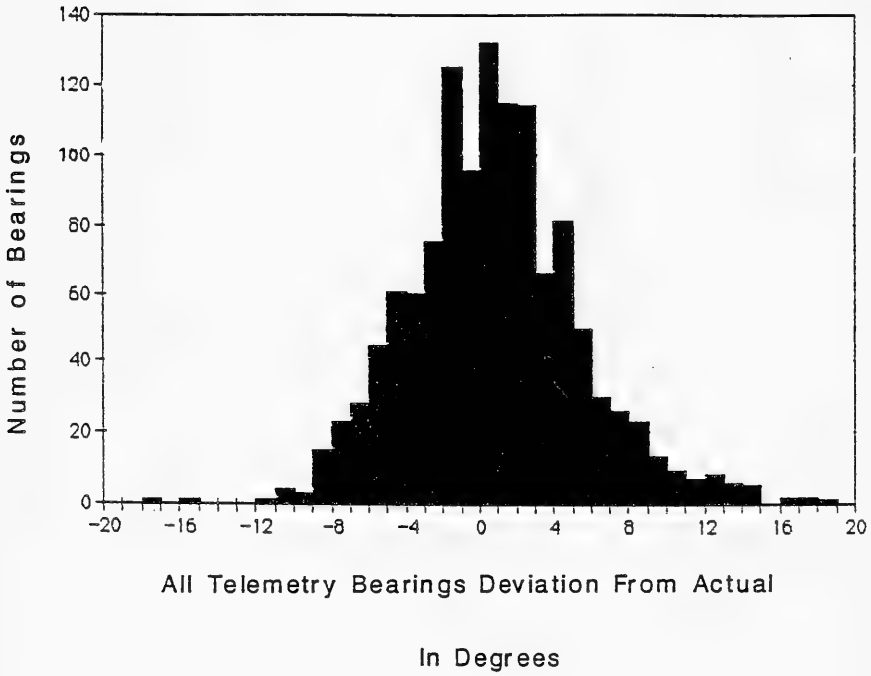


TABLE 7.1 - Summary statistics for the 897 hand-held compass bearings to the signals from the radio transmitters on buoys off the California coast.

	N	Mean difference from true bearing (degrees)	Standard deviation (degrees)
All bearings	897	0.5	4.2
By buoy location:			
South	447	-0.7	4.4
North	450	1.6	4.0
By van:			
1	597	0.5	4.3
2	300	0.5	4.1
By observer:			
1	50	-3.6	1.7
2	250	-0.1	3.8
3	297	1.6	4.4
4	300	0.6	4.2
By shore position:			
1 (south buoy)	247	-1.4	4.1
2 (south buoy)	100	0.3	4.4
3 (south buoy)	100	0.3	3.7
4 (north buoy)	300	2.0	4.1
5 (north buoy)	150	0.8	3.5

TABLE 7.2 - Summary of the calculated precision and accuracy of the methods used to judge the locations of radio transmitters on buoys, based on hand-held compass bearings to the direction of the radio signal and details of the locations of the transmitters on the buoys and the mobile receivers near which the bearings were taken.

A. Precision

South buoy location

N	100
mean size of the 95% confidence ellipse	.03 hectares
standard deviation	.01 hectares

Simulated North buoy location

N	50
mean size of the 95% confidence ellipse	.08 hectares
standard deviation	.02 hectares

Accuracy

South buoy location

N	100
mean deviation from actual transmitter location	51 meters
standard deviation	32 meters

Simulated North buoy location

N	50
mean deviation from actual transmitter location	110 meters
standard deviation	66 meters

B. Distance to transmitter

South buoy location

receiver location 1	700 meters
receiver location 2	600 meters
receiver location 3	613 meters

Simulated North buoy location

receiver location 1	1642 meters
receiver location 2	780 meters
receiver location 3	1262 meters

Degrees between locations

South buoy location

receiver location 1-2	34 degrees
receiver location 2-3	78 degrees

Simulated North buoy location

receiver location 1-2	74 degrees
receiver location 2-3	52 degrees

TABLE 7.3 - Comparisons between the field method of plotting data and the Andrews estimator for the same set of data.

	Field method	Andrews estimator
South buoy location		
N	100	100
mean deviation from actual transmitter location	51 meters	51 meters
standard deviation	37 meters	32 meters
North buoy location		
N	50	50
mean deviation from actual transmitter location	119 meters	110 meters
standard deviation	57 meters	66 meters

deviations greater than we observed. For example, in flat terrain, Hupp and Rati (1983) recorded mean errors between 0.4 and 3.2 degrees, with standard deviations of 1.3-5.0 degrees. In areas with mountains and trees, their estimates of mean error were greater: 4.5 to 28.2 degrees, with standard deviations of 52.7-83.8 degrees. Lee, et al., (1985), taking bearings from fixed towers, reported mean errors between 1.76 and 5.27 degrees (after removing all bearing errors greater than 10 degrees from the sample); Brewer (1983) found that 25%-40% of his bearings were unusable due to the inability to distinguish between direct and reflected signals, and Garrott, et al., (1986) noted that 52% of transmitter locations that were not along the line-of-sight to the position from which bearings were taken, resulted in bearings with large mean errors and/or large standard deviations because of signal reflection.

As shown by the results of these other studies, signal bounce and interference from rugged terrain and obstructions are often major problems during field studies using telemetry. The preferred position to take bearings toward a signal is from a topographically elevated site with a direct and unobstructed line-of-sight to the transmitter. In our study, we often had nearly ideal conditions for telemetry, as many of the positions along the coast from which we took bearings were located at the top of shoreline cliffs, above the transmitters in the otters on the surface of the ocean, and there were no obstructions between the receiver and the transmitter. These conditions minimized the possibility for signal bounce. The bearings which were taken toward the north buoy were taken from positions chosen to be most likely to produce signal bounce. Specifically, the positions of the tracking vans with the receivers were 4 and 6 kilometers from the buoy, so that the bearing direction to the buoy was almost parallel to the general direction of the coast and provided the maximum possibility for interference from intervening land forms. As the error of bearings taken under these conditions was not significantly different from those taken towards the south buoy location, where the bearing direction was towards the open ocean and there were no obstructions, we believe that signal bounce was not a significant source of error in the collection of telemetry location data on the California sea otter.

The accuracy and precision that we calculated are applicable to otters located within approximately 800 meters from shore. At least 75 percent of the plotted locations of adult male and female and juvenile female otters fell into this category (Chapter 3, Fig. 3.8). However, since juvenile males were often located more than 800 meters from shore, the accuracy and precision of our locations for this class of

otters are probably considerably worse than our calculated values.

It should also be realized that our calculations of accuracy and precision represent the error present under ideal conditions, when the radio signals are clear, continuous, and strong and observers are attempting to take optimum readings. Under field conditions, signals are frequently interrupted or weak -- this is particularly likely to be true for those from juvenile males far offshore -- and observers are sometimes tired or hurried.

The locations estimated by the field method of hand-plotting, using bearings from the buoy data sets, were as close to the actual buoy location as the Andrews estimator calculated by program TRIANG (Table 7.3). However, the estimate of the average distance between the hand-plotted locations and the Andrews estimator, using bearings on actual otters, was 162 meters. However, this mean difference cannot be used to quantify the error of the otter locations we estimated in the field, as there are a variety of possible spatial relationships between the two estimated locations. For example, if the actual location of the sea otter is in between the location estimated by the field method and the one indicated by the Andrews estimator, then the difference between the location plotted in the field and the one resulting from Andrews estimator will exceed the distance from either of these estimated points to the actual otter location. Conversely, if both estimated points lie on the same side of the otter's actual location, then the distance between the Andrews estimator and the field estimate could be less than the distance of either to the otter. The distributions of both the points produced by the Andrews estimator and those produced by the method we used in the field in relation to actual otter locations are unknown. The distribution of the Andrew estimator would be dependant upon the differential weighting to bearings given by program TRIANG. We believe, therefore, that it would be inappropriate to add the 162-meter mean difference between these two estimates to our estimate of accuracy.

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CHAPTER 8

MOVEMENT PATTERNS OF ADULT FEMALE AND WEANLING SEA OTTERS IN PRINCE WILLIAM SOUND, ALASKA

C. MONNETT AND L. ROTTERMAN

NOVEMBER 30, 1988

INTRODUCTION

The tendency for sea otters (Enhydra lutris) to exhibit spatial segregation of the sexes is a well established feature of their social system (Lensink 1962; Kenyon 1969; Peterson & Odemar 1969; Schneider 1978; Garshelis & Garshelis 1984; Garshelis, Johnson & Garshelis 1984). Males and females segregate into geographically discrete portions of habitat that are generally referred to as "male areas" and "female areas" (Kenyon 1969, p. 208) or "breeding areas" (Garshelis, Johnson & Garshelis 1984, p. 2648). Male areas are occupied almost exclusively by males of all ages (e.g. Kenyon 1969; Garshelis, Johnson & Garshelis 1984) whereas, female areas tend to contain a mixture of mature males and females of all ages.

The movement patterns of mature males and/or males in the male areas are relatively well understood as a result of tagging and short-term radio-telemetry studies. Young males are born in female areas. In Alaska they apparently leave their natal female areas shortly after weaning. They move to and reside within a single male area or travel among several male areas until maturity (e.g. Kenyon 1969; Garshelis, Johnson & Garshelis 1984), which occurs at about 5-6 years of age (Green 1978; Schneider 1978; Garshelis 1983). As adults, males may re-enter the female areas, wherein they may employ one of two non-mutually exclusive reproductive strategies. The most conspicuous of these two strategies is that of males that defend territories. Territorial males may copulate in serial fashion with females that enter their territories (Vandevere 1970; Calkins & Lent 1975; Loughlin 1977; Garshelis & Garshelis 1984; Garshelis, Johnson & Garshelis 1984; but see Kenyon 1969). Other males, or possibly the same males on other occasions, may opportunistically search for and attempt to pair and/or copulate with females (Kenyon 1969). Reproductive activities normally are concentrated during the fall but some males may remain on their territories year-around. Others return to the male areas (Garshelis, Johnson & Garshelis 1984) where they rejoin the male aggregations and remain until the following breeding season.

Less is known about the movement patterns or distribution of females that reside within the female areas. Short-term studies of individuals, using radio-telemetry, suggest that females are somewhat less mobile and less gregarious than their male counterparts (e.g. Garshelis, Johnson & Garshelis 1984). However, available data have been inadequate to indicate how the female areas are used by individuals or to permit evaluation of variation in females' movement patterns associated with seasonal or functional (e.g. breeding, pupping, wintering, etc.) needs. Also, little information has

been available on the movements of weanlings and on the manner in which they become established within their respective male and female areas.

This chapter describes the movement and habitat use patterns of mature female and immature male and female sea otters in Prince William Sound, Alaska. The movements of adult females are examined at different stages of the reproductive cycle. The movement patterns of weanling males and weanling females are contrasted and discussed in the context of the evolution of dispersal patterns. The relationships between the observed movement patterns and the sea otter's social system are considered.

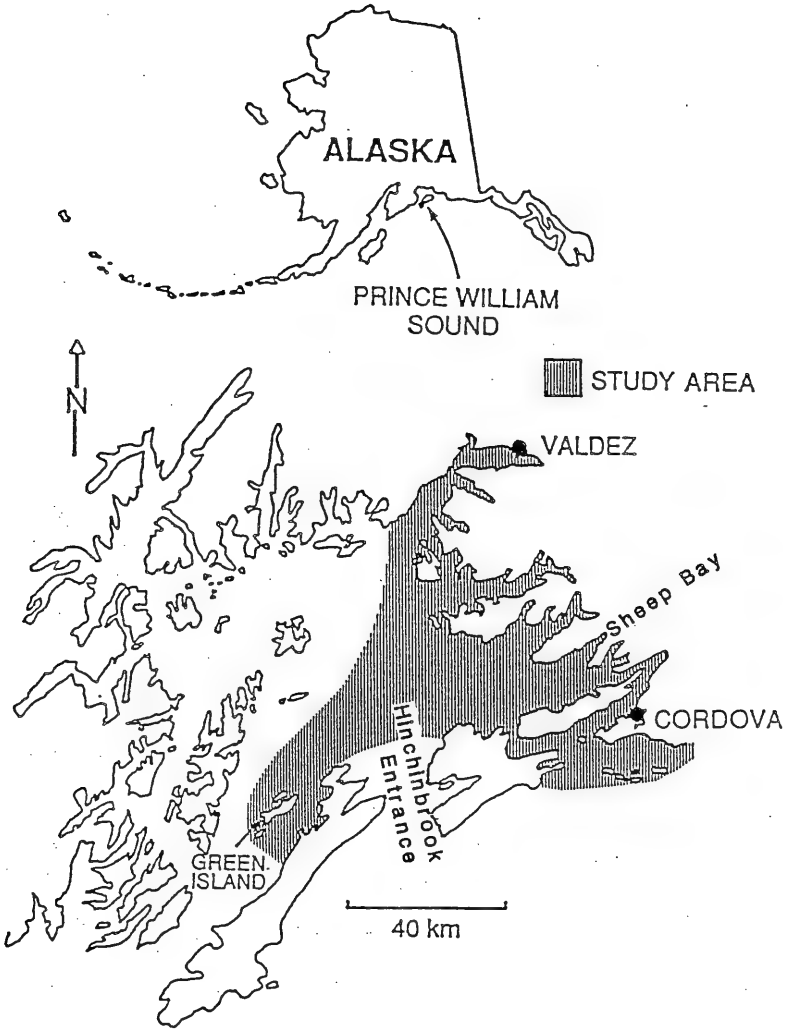
STUDY AREA AND METHODS

The study was located in the eastern portion of Prince William Sound, in south-central Alaska (Figure 8.1). During the past decade, sea otters have recolonized the deep bays, mud flats and channels that are located to the west of the fishing community of Cordova. The local population of sea otters, its history and its habitat have been described by various authors (Calkins & Lent 1975; Siniff, Williams, Johnson & Garshelis 1982; Garshelis & Siniff 1983; Garshelis 1983; Garshelis & Garshelis 1984; Garshelis, Johnson & Garshelis 1984; Garshelis, Garshelis & Kimker 1986).

Data were collected during 18 months between June, 1984 and October, 1986. The subjects included 8 adult females and 35 pups (and indirectly their mothers) from 2 cohorts; 14 during 1984 and 21 during 1985. All otters were captured in Sheep Bay or Simpson Bay. Adults and a few dependent pups were captured in floating tangle nets (91 m long by 5 m deep with a 22 cm stretch mesh) during June, August or September 1984. Most dependent pups were captured in dip nets during August or September, 1984 or 1985. Pups ranged in size from 8 - 20 kg and all still accompanied their mothers. Upon capture, otters were brought aboard a 5.5 m skiff and immobilized with a combination of fentanyl (0.05 mg/kg) and azaperone (0.20 mg/kg) (Williams, Williams & Siniff 1981). Each otter was weighed and its sex was recorded. One or more nylon tags were inserted through the interdigital webbing of one, or both, hind flippers for identification. A radio-transmitter was surgically implanted in each animal's peritoneal cavity by a veterinarian, as described in Chapter 1.

Radio-instrumented sea otters were monitored during daylight in August-October and December 1984; April-December 1985; February, May-June and October 1986. Visual observations were made from a skiff or from the shore with binoculars or 50-80X telescopes (Questar Corp., New Hope, PA, USA 18938). Instrumented otters were normally monitored from

FIGURE 8.1 -- Study area in Prince William Sound, Alaska, 1984-1987.



a skiff that was traveling at 20-30 knots. The skiff was equipped with 2 yagi antennas mounted on 4-m aluminum masts. Antennas were attached at 60 and 300 degree angles from the plane of the boat. Periodically, (approximately 250 total flight hours), instrumented sea otters were monitored from small aircraft that were equipped with 4-element yagi antennas mounted under each wing (Gilmer et al., 1981). Aircraft speed was set at about 100 knots and preferred altitude was 600-750 m.

Radio-transmitter frequencies were scanned on a 2000 channel programmable scanning receiver (Cedar Creek Lab). Radio fixes were determined by triangulation or by moving the boat in the direction of the radio signal until the individual was observed. Otter locations (fixes) were recorded either as coordinates of the Universal Transverse Mercator Grid System, or marked directly on large scale maps or tracings of the various bays and channels. The latter were used predominantly during aerial surveys. Distances were measured on U.S.G.S. scale 1:250,000 or 1:63,360 contour maps.

As Garshelis & Garshelis (1984) pointed out, the annual home range of Prince William Sound sea otters is composed of numerous centers of activity connected by long travel corridors. The area of any portion of the annual home range, or rather, any cluster of fixes, can be estimated by measuring the area of the minimum convex polygon enclosing the fixes (Odum & Kuenzler 1955; Garshelis & Garshelis 1984). In Prince William Sound, sea otter travel corridors often cross, and enclose, deep, broad, and presumably, inhospitable expanses of water. As a consequence, the same procedure, when applied to estimation of annual home ranges, drastically over estimates areas. The large number of fixes required for characterization of such habitat utilization patterns, at least 40 per activity center (Garshelis & Garshelis 1984), makes an accurate measurement of annual, or longer-term, home range impractical. Garshelis & Garshelis (1984) suggested an index of home range: "distance between extreme locations" (DBEL). Herein, it is used to describe the magnitude of the movements of individuals. The distance between extreme locations is the minimum distance an otter would have to swim to go between its two most widely spaced fixes during some time interval. It is approximately equivalent to the maximum dimension of the home range (Garshelis & Garshelis 1984).

RESULTS

Adult female home ranges

Eight adult females were implanted and monitored for periods ranging from 15-20 months. All eight females survived the duration of the study. Four gave birth to pups. All

study females traveled extensively throughout the eastern Prince William Sound. The median distance between extreme locations of the eight females was 41 km (range 27 - 85 km) (Figure 8.2).

Some females made long, circuitous trips which crossed major bodies of water. During the summer of 1985, one female (84001) traveled beyond the limits of the area that was routinely monitored (Figure 8.3). Contact was lost in mid-May and reestablished on October 31. On that date she was near Green Island. She had returned to Sheep Bay by November 7. The short time interval between sightings, at two distant locations, suggests that Hinchenbrook Entrance was traversed. Hinchenbrook Entrance is a channel that spans 11.5 km at its narrowest and is over 300 m deep at its shallowest crossing. It has rapid tidal currents and intemperate conditions. The only alternative to crossing that channel, or other comparably deep, broad channels would have been for female 84001 to have circumnavigated Prince William Sound, a minimum trip in excess of 200 km. All study females traveled between major bays. Most traveled across large expanses of deep water. However, if other study females journeyed beyond the limits of the regularly monitored portions of the study area, they must have done so for only brief periods, since all were located regularly with no comparable periods of lost contact.

The study area was divided into 12 habitat zones in order to illustrate the movements of the eight study females (Figure 8.4). All of the females traveled in four, or more, zones (range 4 - 9) during the time they were monitored (Figure 8.5).

Females tended to occupy the western portions of the study area during the late spring and summer but to travel to the easternmost area where they spent the late fall and winter (Figure 8.6). The eight radio-implanted females used superzone A heavily during May, June and July. At that time most females were pupping or tending small pups (Chapter 9). Females were aggregated into rafts (often containing over 100 individuals) in shallow, protected coves and over shoals. During the fall, many females moved into the bays on the north side of the study area (superzone B). They formed less dense aggregations, weaned their pups and presumably, in some cases, mated with resident males. As winter approached, females became rare in superzone A. This may have been in response to winter storms which often batter those coastlines from the east or northeast. During the late fall and winter, females became abundant in zones 5, 8, 10 and the western portion of zone 9.

FIGURE 8.2 -- Distances between extreme locations of eight adult female sea otters in eastern Prince William Sound, Alaska. The number of fixes and total monitoring intervals are given: # fixes / # days.

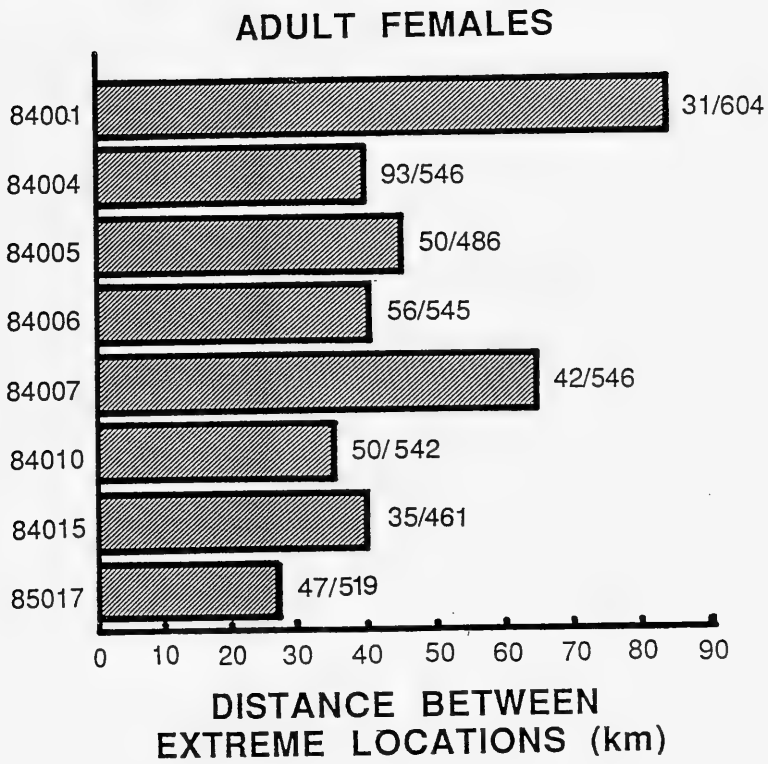


FIGURE 8.3 -- Movements of an adult female sea otter in Prince William Sound, Alaska, during a 20 month interval, June 1984 - February 1986. Summers were spent in the western portion of the study area and winters in the eastern portion, near the Cordova male area.

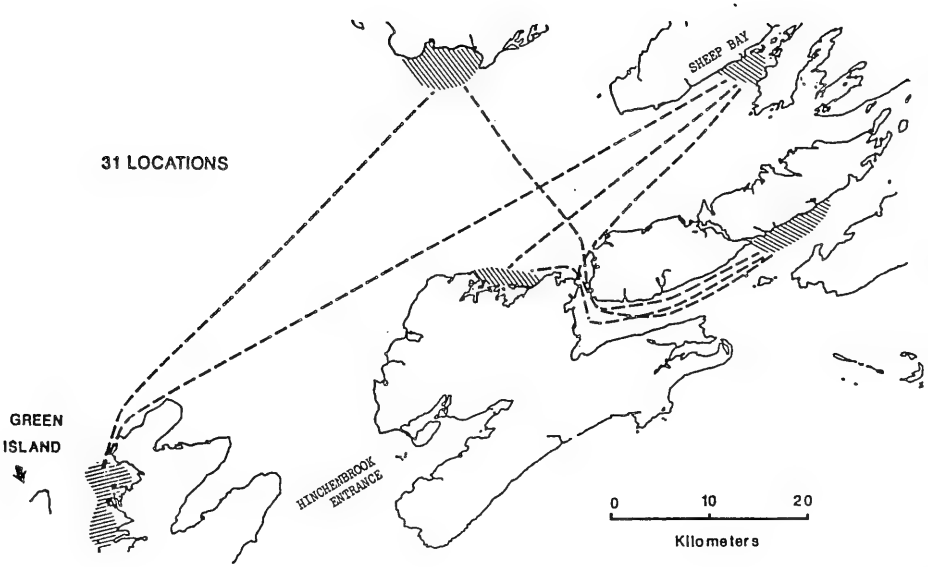


FIGURE 8.4 -- Division of study area in Prince William Sound, Alaska, into numerically designated habitat zones and superzones. Zones correspond to major bays or passages.

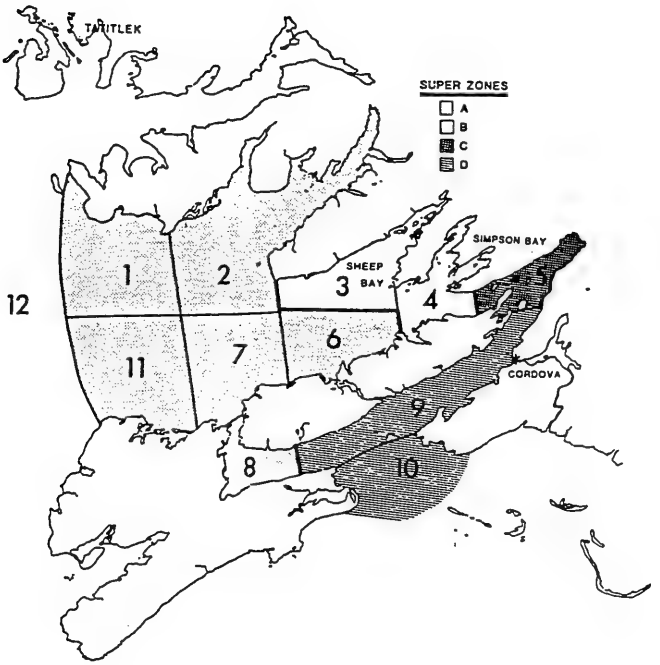


FIGURE 8.5 -- Use of habitat zones in Prince William Sound, Alaska, by eight radio-instrumented adult female sea otters.

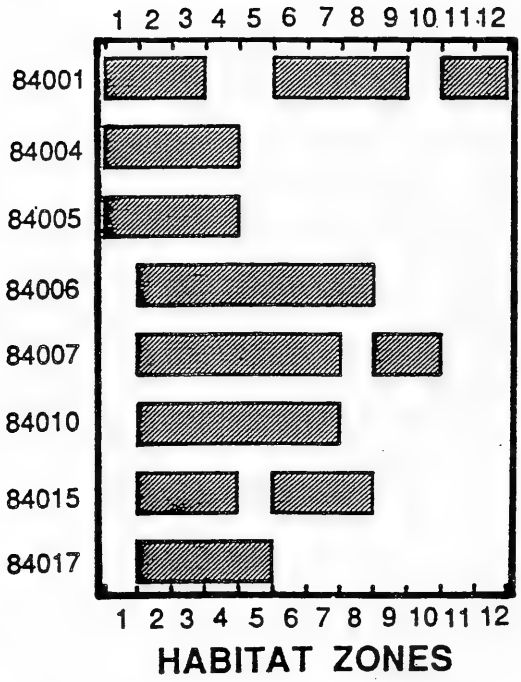


FIGURE 8.6 -- Seasonal changes in the use of portions of eastern Prince William Sound by eight radio-instrumented adult female sea otters. Superzones are delineated on Figure 8.4.

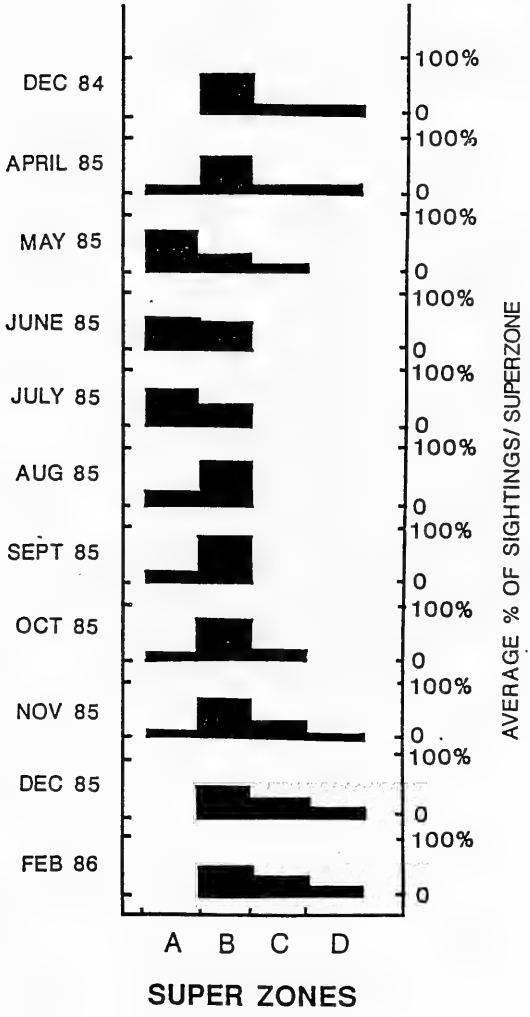
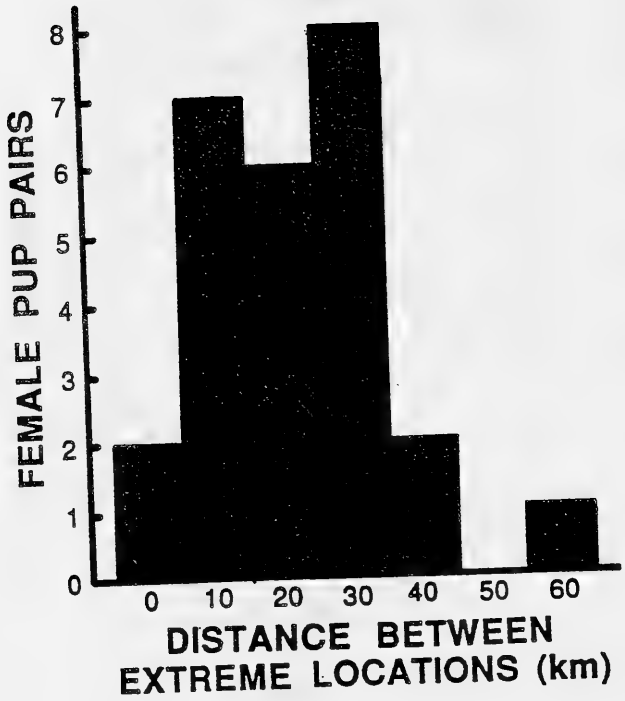


FIGURE 8.7 -- Distance between extreme locations of 26 female sea otters in Prince William Sound, Alaska, that were accompanied by dependent pups. Most observations are based on females accompanying radio-instrumented pups.



Females with pups

Females traveled extensively while they were accompanied by a pup (Figure 8.7). The median distance between extreme locations for females with pups born during 1984 (m = 17.25 km, range = 6.5 - 38.5, n = 10) was shorter than that of females with pups born during 1985 (m = 33 km, range = 15 - 62.5, n = 17). This apparent difference probably resulted from the fact that there are only limited data available on the movements of several of the individuals from 1984. Monitoring was discontinued between late September - mid December, 1984. Consequently, fewer telemetry fixes were available for assessing individual movements during that period than in 1985.

Females apparently only occupied a portion of their annual home range while they were accompanied by pups. Based on data collected on radio- implanted females during 1985, the DBEL of females during the time interval when they were accompanied by pups were smaller than the annual DBEL of the radio-implanted adult females (m = 33 km vs. m = 41 km, Mann-Whitney U test, $p < .02$). This was probably because the formers' home ranges did not include the wintering areas in the eastern portion of the Sound. Accompanied females confined their movements to trips between the western nursery areas and the north-central bays where most weaning took place. Weaning occurred before movement into the wintering areas.

Movements during the last month before weaning.--During the last month before a pup was weaned, the female and pup usually occupied a relatively small, shallow cove or channel. It can be inferred that the pair's home range was smaller, since the distance between extreme locations was shorter than it was during the earlier portion of the dependency period (Figure 8.8). Data for both sexes of pups are pooled for analysis, since data for male and females are similar (last 30 days: $t = -0.17$, N.S.; earlier interval $t = -0.91$, N.S.).

Potentially, there are two ways that the observed differences in home range size could be an artifact of sampling design. The first relates to the relative sample sizes, the second to differences in timing between the respective samples.

First, it has previously been shown that home range area is correlated with the number of fixes analyzed when sample sizes are small (under 40 fixes) (Garshelis & Garshelis 1984). Those authors also found estimated home range area to be correlated with monitoring interval. Thus, if the number of fixes and monitoring intervals were not about the same in the "last 30 days" and "earlier" samples, any differences could

be an artifact. Two arguments can be made against such a problem distorting patterns in the data from this study. One is that the sampling interval and the number of fixes were similar in the two treatments described; sampling interval: last 30 days, mean = 25.6 days (SD = 4.5), earlier, mean = 28.6 days (SD = 11.6); number of fixes: last 30 days, mean = 8.9 (SD = 3.0), earlier, mean = 10.2 (SD = 4.0). The other is that no correlation existed between extreme locations within the pooled samples ($r = -0.03$, N.S.; $r = .21$, N.S., respectively).

Second, since most weaning took place in the late fall (Chapter 9), one reasonable argument could be that shrinking home ranges result from the tendency for adult sea otter females to move into protected areas and to restrict their movements at the onset of winter weather patterns. This does not appear to be the case. Independent females continued to travel, and thus, had large home ranges during the late fall and winter. The distance between extreme locations was longer for independent females, at that time, than it was during the last 30 days before weaning for female-pup pairs ($m = 19.5$ km, $n = 8$ vs. 7.5 km, $n = 19$, respectively; Mann-Whitney U-test $p < .02$).

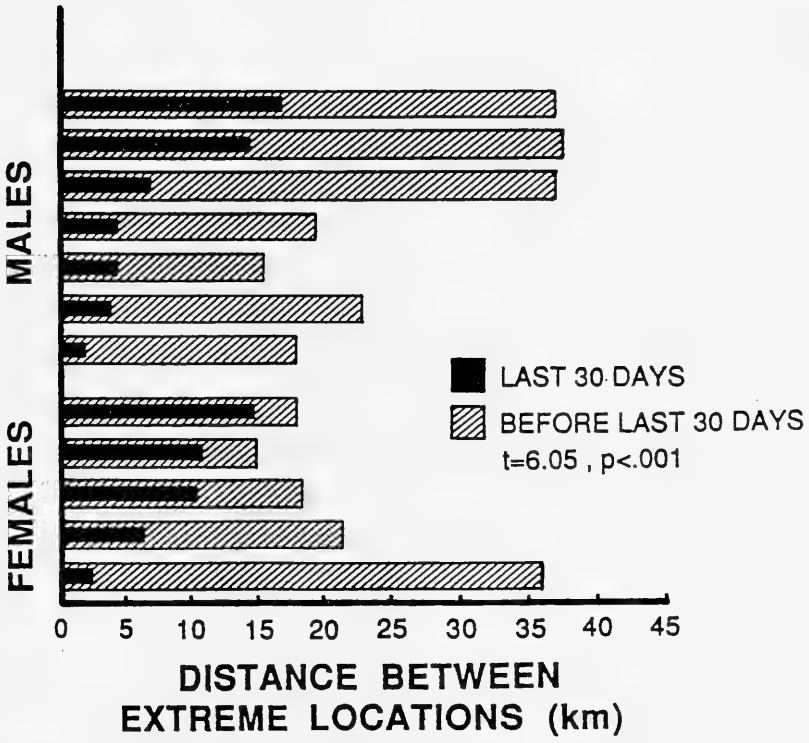
Sexual differences in adult home range size

A direct comparison can be made between the extent of movements of adult males and adult females, within northeastern Prince William Sound, by combining the results of this study with those of the earlier studies of Garshelis and Garshelis (1984, p. 674, Fig. 7). Those authors argued that male home ranges were larger than female home ranges in Prince William Sound. However, they pointed out that at least part of the difference could have been due to females' movements being constrained by geographic boundaries. That is, female areas at Green Island, in central Prince William Sound, were smaller than male areas in Nelson Bay, in northeastern Prince William Sound. Thus, a comparison of males and females in the same general area (i.e. within northeastern Prince William Sound) should be a better test for sex differences in movements.

As mentioned above, the relative number of fixes during each study and the durations of the studies could affect the results. Thus, an attempt was made to ensure that the data from the two studies were directly comparable. Only data from the July - Sept. interval, 1-3 months of monitoring, are considered. However, data from the latter study includes that on both independent females and females with pups.

To test for differences in movements of adults, the proportions of males and females in 2 distance categories

FIGURE 8.8 -- Changes in the home ranges of sea otter female-pup pairs in Prince William Sound, Alaska, that occur as the pups approach weaning age. The distances between extreme locations of pairs are compared for the last 30 days before weaning and for the earlier period when the pup was younger.



were compared: individuals with DBEL < 15 km and those with DBEL > 15 km. The DBEL of adult females were larger than those of adult males (respective ranges 15 -60 km vs. 4.8 - 37 km; Chi square = 14.31, 1 DF, $p < .001$).

The sea otter population of Prince William Sound is still increasing after near extirpation by fur traders during the end of the 18th century (Lensink 1962). The history of the local remnant population is fairly well documented. Simpson Bay, in zone 4, and superzone C went through a transition from being a male area to being a female area in the early 1980's (Garshelis & Garshelis 1984; Garshelis, Garshelis & Kimker 1986; this study). By 1986 the male area was entirely contained within superzone D. The eastern Prince William Sound contained but a single, well consolidated male area which was surrounded by female areas. At its eastern edge, in zone 10, the population was dominated by females. That area was heavily used by females, some of which were accompanied by dependent pups, during the winter and spring 1984-1987.

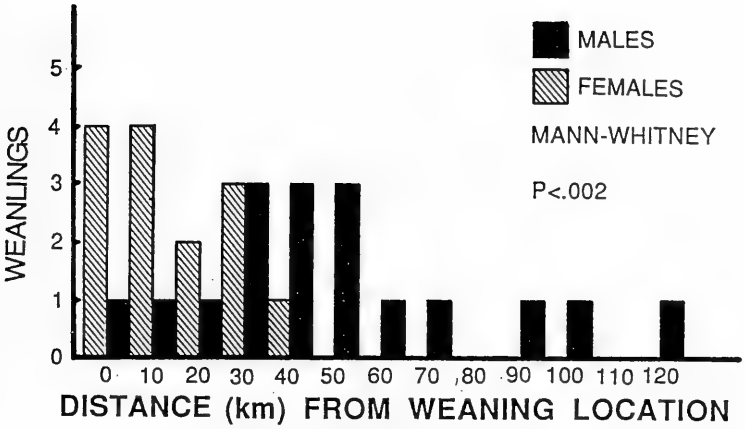
Movements of weanlings

Most pups were born during May and weaned during the subsequent fall (Chapter 9). Two characteristic movement patterns were exhibited by sea otters during their first year following weaning. Some weanlings stayed within, or very close to, the home range they had occupied during the month preceding weaning. However, most weanlings immediately made a relatively large movement, then occupied a small home range until spring. During spring, they expanded their home range. Their movements within the extended home range took them still further from their site of weaning.

By the end of monitoring (maximum 21 mo.) many of the weanlings had traveled far from the site at which they separated from their mothers (Figure 8.9). Males had moved longer distances than their female counterparts. Mortality was high (Chapter 9). Many of the weanlings' trips had culminated with their death. The next few sections deal with sea otter behavior during their first year of independence.

If weanlings moved significantly from their site of weaning, they almost always began their travels abruptly, within 2 weeks after weaning. For example, 14 weanlings in the 1985 cohort traveled 20 km or more. Within their first two weeks of independence, 13 of the 14 had moved at least 20 km from their weaning location. The 14th weanling also moved abruptly but did not do so until about two months had passed. Most weanlings departed almost immediately following separation. Since departures were abrupt and movements tended to be fairly long, contact was usually lost until a search

FIGURE 8.9 -- Distances traveled from the site of weaning in Prince William Sound, Alaska, by male and female weanling sea otters. Monitoring interval varied from a few days to approximately 18 months. Short monitoring intervals resulted when pups died during their travels.



could be made from an aircraft. By the time that the first post-weaning radio fix was taken, the weanling's travels were usually completed.

Most traveled at least 20 km from where they were weaned to their post-weaning home range. During their first trip males tended to travel further than females (Figure 8.10). Weanlings usually completed their first trip quickly. Data on three weanlings that were weaned during the first week of November, 1985, illustrate this point. Two of these weanlings were males that were weaned on, or at most, a few days before 11/4 and 11/6, respectively. The third was a female that was weaned during the night of 11/6. All departed from their pre-weaning home ranges in Sheep Bay or Simpson Bay on the night of 11/6. Those bays were searched thoroughly from a skiff on 11/7. None of the three were found within the 10 km search radius. An aerial survey was flown on 11/9. The female was found 38 km to the southwest on the far side of Orca Bay. The two males were not located on 11/9. At that time they were not within 50 km of their weaning location. The search area was expanded during a second aerial survey on 11/16. One male was found near Valdez, at a distance of 123 km. The other male had traveled about 80 km along the same coastline. On the next aerial survey of that area, a few weeks later, he was also near Valdez, 109 km from the place where he was weaned.

The extent of weanlings' movements that defined the post-weaning home ranges appeared to vary substantially between individuals. The distance between extreme locations was greater for males than females, however, not significantly (Figure 8.11).

The process of segregation of sea otters into male and female areas figures prominently in early sea otter behavior. When weanling males travel to their first post-weaning home ranges they usually leave the female areas in which they were reared (Figure 8.12). Conversely, young females usually do not leave. In this study, three young females had home ranges outside the female area during their first winter. Two of these females survived until spring, at which time both returned to the female area. Only two of twelve males known to have survived their first winter were not within the male area.

DISCUSSION

The data given in this paper indicate that the extent of movement by sea otters in eastern Prince William Sound varies with age, sex and reproductive status. Relatedly, otters use specific portions of their habitat for different purposes. Thus, densities within a given area can change dramatically

FIGURE 8.10 -- Distance between weaning of sea otters location in Prince William Sound, Alaska, and their first post-weaning home range. The distance was traveled in a single relatively rapid trip.

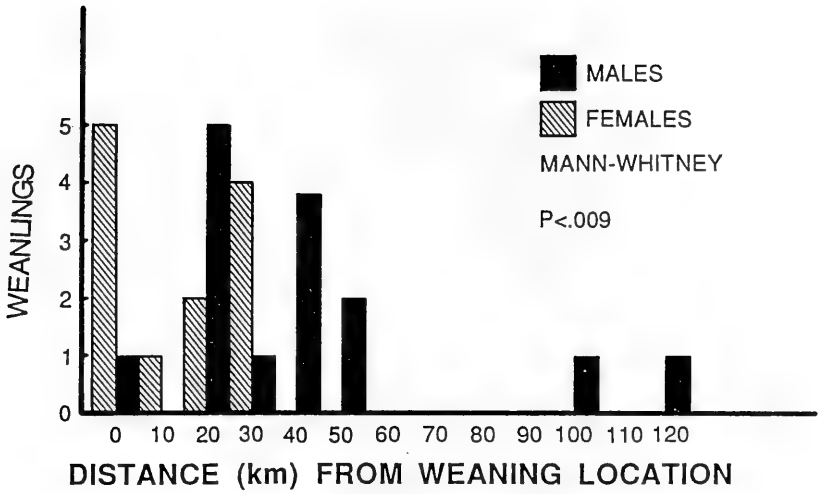


FIGURE 8.11 -- Relative size of weanling male and female sea otter home ranges in Prince William Sound, Alaska, during the first winter following weaning. Only weanlings with well defined home ranges are included.

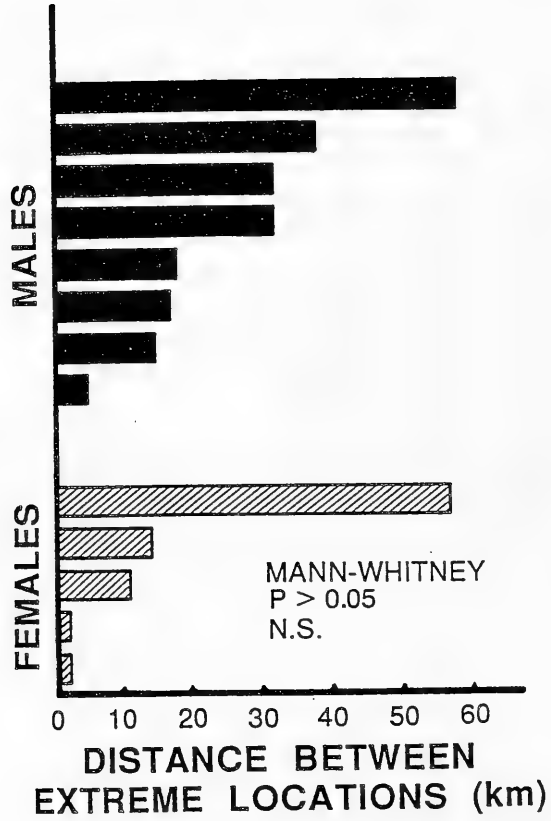
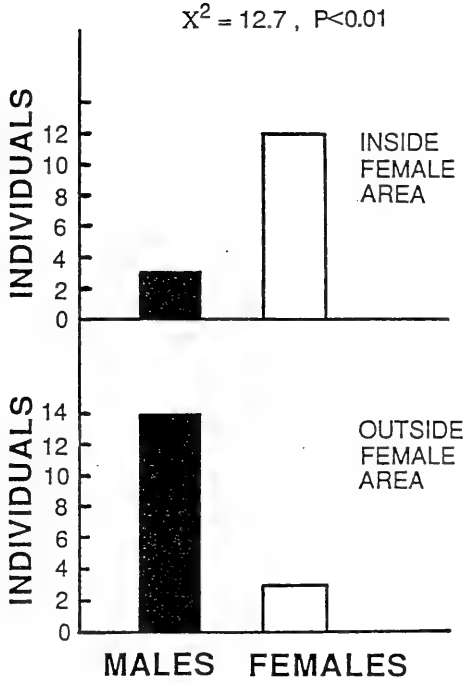


FIGURE 8.12 -- Tendency for weanling sea otters in Prince William Sound, Alaska, to leave natal female area after being weaned. Female weanlings usually do not leave natal female area, whereas males usually do. Female area consists of zones 1, 2, 3, 4, 6, 7, 8, and 11 on Figure 8.4.



over the course of a year. These data also show that sexual segregation occurs very early in life as a result of differences in the behavior of male and female weanlings. Weanlings of both sexes were competent and capable of making considerable movements as soon as they became independent. These observations are discussed below.

Adult movements

The observed movement patterns of the adult female sea otters in Prince William Sound were remarkable for several reasons. Overall, adult females were more mobile than had been anticipated. Individual females used a considerable portion of the total female area. However, both the extent of their movements and their destinations changed seasonally and with the age of their dependent offspring. Adult females became quite sedentary when accompanied by large dependent pups that were close to the age of weaning. They were also more gregarious and exhibited more pronounced seasonal habitat use patterns than suggested by previous investigations.

The median distances between extreme locations (DBEL) of independent females (41 km) and females with dependent pups (33 km) were longer than those measured in previous studies. Kenyon (1969) suggested that the home range of females usually included less than 17 km of coastline. Garshelis and Garshelis (1984) studied independent females at Green Island, which is located about 80 km southwest of the current study area. They measured DBEL that ranged from 2.6 - 15 km. The early studies in California reported female home ranges that were comparatively smaller than those observed by Garshelis and Garshelis (Loughlin 1977; Ribic 1982). None of those studies reported female movements in excess of about 17 km. However, the results of ongoing studies at other locations in Alaska and California (Monnett, 1987) (Chapter 3) suggest that DBEL as long as those observed in this study may be common.

Garshelis and Garshelis (1984) recognized that females were leaving their study area and that their data did not necessarily reflect annual or lifetime home ranges. It is possible that some of the studies that have reported relatively sedentary behavior by females have obtained that result as a function of the study design. If individuals are monitored for periods of a few months or less, large distance movements between functional sub-habitats might not be identified (e.g. breeding vs. wintering area). Seasonal movements have also been suggested for the population that inhabits the Bering Sea along the Alaska Peninsula (Lensink 1962; Cimberg & Costa 1975; but see Monnett 1987b).

Based on a limited number of observations at Green Island, Garshelis & Garshelis (1984) concluded that females

occupied larger home ranges when accompanied by young pups than they did when their pups were nearly ready for weaning. They posited that the change in behavior, as the pups became older, was necessitated by the need for pups to gain experience in self feeding. Such experience could only be gained if movements were restricted to a limited portion of the habitat where water depths were shallow and suitable prey were available. Their hypothesis is consistent with the findings of this study. However, there are no data from this study on pup feeding behavior in weaning, or other, areas.

It is likely that real variation in the movement patterns of adult females exists between the populations of sea otters at separate study areas due to differences in population status, geography or genotypes.

In the eastern portion of Prince William Sound, range reoccupation is still occurring, with subsequent changes in distribution. The Green Island area, where Garshelis and Garshelis (1984) conducted most of their work on female movements, has been occupied much longer and, hence, distributions per se are probably not changing because of recolonization.

In areas where coastlines are complex, the extent of movements could also be constrained by local geography (Garshelis & Garshelis 1984). Relatedly, individuals that inhabit calm waters such as Prince William Sound might find travel less physically demanding and/or less risky than individuals that inhabit more exposed waters such as the Gulf of Alaska or the Pacific Ocean off California. For example, females with pups might find travel difficult if they inhabit waters along unprotected coastlines and, thus, restrict their movements to only the most protected areas (D.B. Siniff personal communication).

Authors have not agreed on the relative extent of movements of males and females. Kenyon (1969) and Garshelis and Garshelis (1984) have argued that males have larger home ranges, whereas Loughlin (1977) and Ribic (1982) reported larger home ranges for females. The significance of these reported differences should be viewed conservatively. It is likely that some comparisons reflect differences in movements that are contained within single male areas or female areas and exclude movements between major habitat units that are of functional significance (e.g. the criticism by Garshelis and Garshelis (1984) of Ribic's (1982) result). It is well documented that individuals of both sexes can make very long movements (> 80 km) between breeding areas and wintering areas (reviewed in Garshelis & Garshelis 1984; this study). Conversely, individuals of both sexes can be relatively sedentary (e.g. territorial males (Garshelis & Garshelis 1984)

vs. females with dependent pups just before weaning (this study)). Mobile and sedentary periods may not coincide in males and females. As a consequence, measures of home ranges are likely to be biased if studies are short term and do not take into account sex-specific seasonal differences in habitat use patterns. General conclusions about sex differences are premature until longer-term data on both sexes are available.

From observations at Green Island, Garshelis and Garshelis (1984) concluded that females formed considerably smaller groups than did males. Indeed, only relatively small groups of females (< 50) were encountered in the vicinity of Green Island during field work conducted during 1985 and 1986 (personal observation). However, recent observations in other parts of Prince William Sound and elsewhere suggest that this conclusion may not be general. Females frequently form large aggregations, well in excess of 100 individuals. Such aggregations have been seen in Prince William Sound (this study), in the Bering Sea along the Alaska Peninsula (Monnett 1987) and in the vicinity of Kodiak Island, Alaska (A. DeGange personal communication). As Garshelis and Garshelis (1984) point out, group size is likely to be related to the type of sea otter activity and local density.

Weanling Movements

Observations during this study indicated that weanlings established home ranges in their respective male and female areas shortly after separation from their mothers. Most weanlings moved a long distance from their site of weaning before doing so. Since pups were weaned in female areas, female weanlings were not required to travel as far as males. Garshelis, et al. (1984) observed a similar rapid departure of male weanlings from natal female areas. However, they also noted that during May-August the age structure of males in male areas had an excess of 2 and 3 year old males (by two to three fold) compared to yearling males. Because of this age structure they suggested that some weanling males may delay entering male areas until after their first year. Observations on radio-instrumented pups in this study do not support that contention. Another way to interpret the age structure observation is that they are observing variation in cohort recruitment. Two observations support this latter alternative. First, there was significant variation in the sex ratio of dependent pups caught in the same area between 1984-1986 (Chapter 9). Yearly differences in male birth rates, or survival rates, could result in corresponding cohort differences in the male rafts. Moreover, the delayed entry hypothesis does not explain the relative lack of 4-5 year old males in the male area observed by Garshelis, et al. (1984). Four and five year old males are generally assumed to be immature and should have been present in the male area in

their actual proportions. The relative scarcity of 4 and 5 year old males is consistent with the notion of varying cohort sizes.

Evidence from other investigations also suggests that weanlings in Alaska segregate into respective male and female areas relatively soon after weaning. Kenyon (1969) reported more juvenile females than juvenile males (53:31) in female areas near Amchitka, in the western Aleutian Islands. Lensink (1962) examined dead juveniles at male hauling grounds and found the sex ratios to favor males (30:6). This ratio seems too extreme to be due to the easier identification of male carcasses in poor condition (see Chapter 6).

The recently independent otters in this study, particularly males, apparently were capable of traveling long distances in a fairly short period of time. Young male sea otters have been observed to make similar long distance movements to male areas in previous studies. Garshelis, et al., (1984) observed a male weanling that left a female area and traveled over 100 km to a male area in Prince William Sound.

Garshelis, et al. (1984) suggested that young male sea otters may move into the aggregations found in male areas because of certain benefits that may be derived from gregariousness. Those authors suggested that benefits may be derived from social facilitation, opportunities for assessment of conspecific competitors, safety from predation and metabolic advantages gained from hauling out on sandbars that exist in those areas. Data on survival rates of weanlings from this study supports the hypothesis that movement from the natal area to a male area may be generally beneficial. Male weanlings, that spent their first winter following weaning in the male area, were more likely to survive than those that remained in the female areas (Monnett 1987).

The relationship between movement data and dispersal

For this discussion we follow the terminology of Greenwood (1980:1141) who distinguished between several common usages of the term dispersal. He defined natal dispersal as that dispersal "...from birth site to first breeding or potential breeding site...". He contrasted natal dispersal with breeding dispersal: "...movement of individuals, which have reproduced, between successive breeding sites..." and effective dispersal: natal or breeding dispersal followed by successful breeding. These definitions are not universally accepted. Rather, the terminology of dispersal has been used inconsistently between authors (e.g. Greenwood 1980 cf. Lidicker 1975; Gaines and McClenaghan 1980; Dobson 1982).

The movement data given herein should not be taken as accurate measurements of natal, effective or breeding dispersal as defined by Greenwood (1980). That is, measures are incomplete because data are not given on the distribution of mature individuals or their breeding sites. These data are of post-weaning movement patterns.

From observations made during this study, it does appear that young females are more conservative in their dispersal movements than males. Several observations support this contention. First, males traveled further than females during the weeks immediately following weaning. The very long movements were all made by males. Moreover, the sex ratio of the individuals with which contact was lost strongly favored males. That suggests that some males may have left the monitored region. Second, males usually left the female area of birth when weaned, whereas females rarely did. Third, juvenile males remained outside the female area as long as they were monitored. Conversely, those females that left the female area following weaning, and that survived the winter, returned to the female area in the spring. Fourth, as juveniles, most males continued to travel further from their weaning location. Females restricted their travels to sites within the female areas.

The observations made during this study do suggest that future interpretations of the relationship between breeding sites and natal sites in sea otter populations are likely to be problematic. In order to evaluate an individual's dispersal, a starting point has to be determined, as well as an ending point. Howard (1960) referred to this starting point as "...its point of origin..." which Greenwood (1980) took to mean its place, or group, of birth. There is little confusion when the young remain at a single location throughout dependency (e.g. nests, dens or burrows) or when they remain within a cohesive social group (e.g. prides, packs or troops). However, as shown in this study, sea otter females travel extensively while accompanied by dependent pups. Consequently, the sites of conception, birth and weaning may not coincide. Any, or all, of those locations could be regarded as the point of origin, depending upon the question under consideration (e.g. inbreeding avoidance vs. site experience).

Available evidence seems to indicate that females stay within their natal female areas, near the areas they inhabited when they accompanied their mothers. However, many leave the immediate location where they were weaned. Conversely, juvenile male departure from the same areas appears to be almost obligate. Only two males out of the 12 that survived their first winter had not left the female area by January. In order to exhibit natal philopatry equal to that exhibited

by female weanlings, males would have to re-enter natal female areas after becoming sexually mature and breed in areas they inhabited with their mothers. However, from the perspective of the juvenile male, any attraction to the natal female area that might result as a consequence of benefits derived from site familiarity or individual recognition (Greenwood 1980) are likely to have been diminished by the length of tenure in the male area. Male sea otters mature and apparently begin to seek breeding opportunities after five or more years of residence in the male area. It would seem questionable whether what was learned about the natal female area during dependency could be retained until the age of potential re-entry. Moreover, even if retained, some of that knowledge would be likely to be obsolete because of changes in habitat conditions during that period (e.g. food abundance, conspecific distributions).

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CHAPTER 9

SEX-RELATED PATTERNS IN THE POST-NATAL DEVELOPMENT AND SURVIVAL OF SEA OTTERS IN PRINCE WILLIAM SOUND, ALASKA

C. MONNETT AND L. ROTTERMAN

NOVEMBER 30, 1988

INTRODUCTION

Pronounced sex differences in morphology, development (Glucksman, 1974, 1978), and behavior (Clutton-Brock and Albon, 1982) exist between the males and females of many large mammals. While the general theoretical explanations for these differences are fairly well developed, there is still little known about the proximate causes or consequences of these differences for most species (Clutton-Brock and Albon, 1982).

According to current evolutionary theory, parental investment (PI) (Trivers, 1972) should be distributed among progeny so as to maximize parental inclusive fitness (sensu Hamilton, 1964). Disproportionate allocation of PI to male or female offspring could occur in situations where the production of one sex has a potentially greater effect on parental inclusive fitness than the production of the other sex. In polygynous mammals, if an inequality is to occur, males should be the favored sex for two reasons: intrasexual competition and male-biased dispersal.

Among polygynous mammals, variation in reproductive success is likely to be greater among males than among females (Trivers, 1972; Clutton-Brock, et al., 1977; Clutton-Brock and Albon, 1982). The allocation of parental resources should favorably influence an offspring's body condition as an adult and thus, its relative ability in intrasexual competition with conspecifics. As a result, if their reproductive success is affected by their competitive ability, individual offspring that receive the most PI during dependency should achieve the highest reproductive success as adults (Trivers and Willard, 1973). Since male mammals generally compete, either directly or indirectly, for access to females, high quality sons are likely to leave more offspring than high quality daughters (Trivers and Willard, 1973). Consequently, females should tend to invest more resources in individual sons than in individual daughters (Clutton-Brock and Albon, 1982).

The pattern of PI in individual male and female offspring could also be influenced by the tendency for one sex to disperse more than the other sex (e.g. Greenwood, 1980). If survival during dispersal is influenced by maternal PI before weaning, females should contribute more PI to progeny of the dispersing sex (Clutton-Brock and Albon, 1982). In most mammals those progeny would be males (reviewed in Greenwood 1980).

Given the typical mating system and dispersal patterns seen in mammals, a unit of PI apparently has a greater potential to effect the survival and the reproductive success of male progeny than female progeny. Thus, more PI should be allocated to dependent males relative to females. This

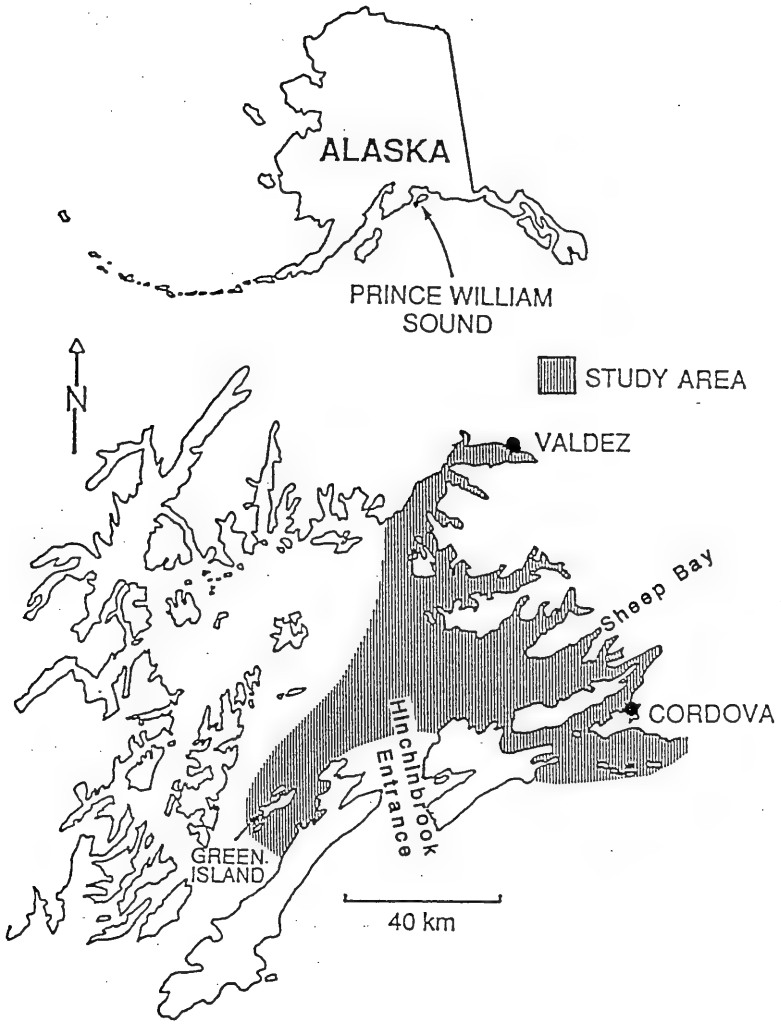
could be accomplished in 2 general ways: First, parents could manipulate offspring sex at conception (Trivers and Willard, 1973). Second, during the period of dependency, parents could preferentially allocate more PI to male offspring than to female offspring (Reiter et al., 1978). For example, males could be given high quality and/or greater quantities of food or permitted to have longer dependency periods.

Sea otters (Enhydra lutris) are a sexually dimorphic, polygynous mustelid that is highly specialized for the marine environment (Kenyon, 1969). They have a resource-defense mating system (Greenwood, 1980) with males occupying and defending breeding territories (e.g., Calkins and Lent, 1975; Loughlin, 1977; Garshelis and Garshelis, 1984). In Alaska, males tend to leave the area in which they were reared at the end of parental care, whereas females do not (Chapter 8). A radio-telemetry study was conducted from 1984-1987 in order to investigate differences in juvenile development and behavior, with specific focus on differences between the sexes. Comparisons are made of time of birth, growth rates, dependency periods and mortality patterns. Under the theoretical arguments reviewed above, male sea otters should be born earlier in the spring, grow more rapidly and have longer dependency periods. Differences in post-weaning behavior between sexes, especially in movement patterns, might subject juvenile males and females to different risks. Since male sea otters travel farther from their weaning site, they should be subject to greater risk and exhibit correspondingly higher mortality during the first few months following weaning.

STUDY AREA AND METHODS

Studies of sea otter pups and weanlings were carried out in two general areas within Prince William Sound (PWS) in south-central Alaska (Figure 9.1). Observations were made in the northeastern portion of the Sound during 1984-1986. Observations were made at Green island, in the south-central sound, during the summer of 1985. Research activities were coordinated from cabins in Sheep Bay and on Green Island, within the Sound, and from a United States Fish and Wildlife Service warehouse and University of Alaska marine advisory office in Cordova. The local population of sea otters, its history, habitat and ecology, have been described by a number of authors (Calkins and Lent, 1975; Siniff, et al., 1982; Garshelis and Siniff, 1983; Garshelis and Garshelis, 1984; Garshelis, et al., 1984; Garshelis, et al., 1986).

FIGURE 9.1 -- Location of study area in Alaska and Prince William Sound, 1984-1987.



Pup capture

Pups (N=157) were captured for routine tagging and data collection with dip nets and tangle nets. Several types of nets, including commercially available salmon dip nets, were tested. The most satisfactory results, and the most pups, were obtained by using a custom fabricated, aluminum dip net (Alaska Power Services, Cordova, Ak 99574). This net was characterized by a long (4m) handle and semicircular "basket" that attached to the handle at a 90 degree angle. Mother-pup pairs were pursued in a Boston Whaler skiff (5.5 M) until the pair surfaced near the bow. The basket of the net was then dropped in front of the moving animal(s) and drawn, with the pup, up and back over the bow of the boat, the pup captured in the net. Large pups were usually not carried by their mothers and, since they were generally incompetent divers, were easily netted. Smaller pups were carried by their mothers as they made repeated dives. Successful captures usually occurred in 3 circumstances: 1. The mother was caught as she carried the pup, separated from the pup and released. 2. The pup was separated from the mother by drawing the net between the pair, over the pup, as they surfaced for air. 3. The mother released the pup after a few dives and it was scooped as it floundered on the surface. Exceptions to the above scenarios included a few mothers (less than 10%) that abandoned their pups on the surface immediately on the approach of the boat and a few cases when mothers were on foraging dives when their pups were captured.

Pup handling

Upon capture, each pup was tagged with numbered, nylon Temple or button tags (Ames, et al., 1983) in the interdigital webbing of one, or both, hind flipper(s). The weight, length and sex were recorded. Weights were taken in pounds because equipment was available only with those scales. The unevenness of some of the values assumed for calculations reflects the conversion of those measures to metric scale. Pups were weighed to the nearest 0.5 pound, with the exception of the newborns that were weighed to the nearest 0.25 pound. Pups were held for 5-15 minutes depending upon whether a blood sample was taken.

Pup release

Pups were released into the water and generally observed until they reunited with their mothers. If the mother was not near the boat when a pup was to be released, cassette playbacks of pup vocalizations (loud cries) were used as an attractant. Mothers appeared not to discriminate between the sounds of their own pup and those of others. The recorded cries of a single pup were used effectively on many different

mother-pup pairs. Females were attracted to the boat with these playbacks from distances of over 1/2 km. Pups also responded to the playbacks by swimming toward the boat and, on some occasions, crying back. They were particularly indiscriminate and often could be stimulated into lengthy conversations by crude, human imitations of their own cry.

Recaptures

Forty-one dependent pups were recaptured on at least one occasion. Previously caught pups were selected for capture and identified by their flipper tags. They were captured and handled as described above. Capture activities were usually spaced to insure that intervals of 30-70 days had passed between successive captures so that growth rates could be determined.

Telemetry

Radio-transmitters were surgically implanted in the peritoneal cavity of 37 dependent pups, during August or September, 1984 or 1985, by veterinarians, as described in Chapter 1. Most pups weighed 9-14 kg when implanted (range 7-20 kg).

Upon capture, pups were brought aboard a 5.5 m skiff, weighed and immobilized with a combination of fentanyl (generally 0.05 mg/kg) and azaperone (0.20 mg/kg) (Williams, et al., 1981). Naloxone (0.01 mg/kg), an antagonist to fentanyl, was injected in all subjects following surgery, but before release. Pups were released into the water near their capture site and generally were observed until they reunited with their mothers. Normally less than 60 minutes elapsed between an animal's capture and release. Playbacks of pup cries, as described above, were used to keep mothers attentive and near the boat during pups' surgeries.

Radio-implanted otters were monitored from small aircraft or small boats equipped with yagi antennas and 2000 channel, programmable scanning receivers (Cedar Creek Bioelectronics Lab). Radios had ranges of 1-5 km and 6-10 km when monitored from boats and aircraft, respectively. An attempt was made to observe most pups 1-2 times per week during the fall, before they became independent.

The transmitters had a maximum life expectancy of about 700 days. One-hundred twenty-five transmitters of the same design were implanted in sea otters in Alaska and California, between March, 1984, and September, 1986. To date, only two are believed to have malfunctioned and many have operated 500 days or longer. The durability of the units is evidenced by the recovery of 14 operating transmitters from intertidal

marine areas at various times following the deaths of the subjects. Some were found buried under boulders on beaches and had been subjected to heavy surf. One radio was still operating after at least 13 months on a gravel beach, in the intertidal, near Valdez.

Birth date estimates

Sea otter births are seldom, if ever, observed in natural situations. Consequently, birth dates for pups must be estimated. Such estimates can be based upon pup weight at capture, if information is available about normal birth weights and about pup growth rates (Wendell, et al., 1984). If relevant data are not available, assumptions must be made about birth weights and growth rates, based on population averages.

For estimates given here, birth weight was assumed to be approximately 4.5 lb (2.04 kg). This value was chosen based on several types of information available from sea otters in Alaska. First, 2 kg approximates the average birth weight observed in this study. Second, based on his observations of fetuses and newborns in a population near Amchitka, Kenyon (1969) argued that "normal" birth weight is between 1.87 and 2.3 kg. Third, Schneider (1978b), used the same types of data to estimate that the mean birth weight in the central and western Aleutian Islands was 1.8 - 1.9 kg. It is important to note that individual variation in birth weight has little effect on the accuracy of birth date estimates since growth rates are fast. An error of several hundred grams would only change the estimated birth date by a few days.

Based on data from this study, growth rates are assumed to be approximately 95 g/day (0.21 lb) for males and 86 g/day (0.19 lb) for females. No other growth rate data are available for sea otters in Alaska.

Dependency period estimates

Dependency periods for the radio-implanted pups were calculated from estimated birth dates and separation dates. In order to do this, several assumptions were made. As noted above, birth weight was assumed to be 2.04 kg. Actual growth rates were used for those pups that had been recaptured and hence, had been weighed on two or more occasions. If multiple weights were not available, it was assumed that females gained 86 g/day and that males gained 95 g/day. In these cases, estimated birth dates were bracketed by estimates made by assuming growth rates of plus and minus 1 standard deviation (SD).

Survival rates

Survival estimates, based on telemetry data, were calculated using the method developed by Trent and Rongstad (1974).

Separate survival estimates were calculated for males and females during pre-weaning and post-weaning intervals. Since the exact day of death was rarely known, two survival-related calculations were made. In the first calculation, it was assumed that the animal died the last day it was seen alive. In the second calculation, it was assumed that it died the first day it was known to be dead. In some instances individuals became missing but it was not certain whether the cause was death, dispersal or radio failure. Thus, the suggestion of Heisley and Fuller (1985) was followed and two survival rates were calculated. In the first, it is assumed that missing individuals were dead; in the second, that they were alive.

One pup died shortly following surgery as a result of a veterinary error. This pup is not included in estimates about survival since it is unlikely that the error will be repeated, and thus the case is not relevant to understanding normal survival probabilities or factors influencing survival schedules.

RESULTS

Birth weight

It was assumed that pups were newborn if pink umbilical fragments were still attached when they were captured (Kenyon 1969). Three such newborn pups had weights and total body lengths of 1.7 kg and 48 cm, 1.8 kg and 50 cm and 2.4 kg and 55 cm, respectively. Three other small pups were captured that had no trace of umbilical fragments. These measured 1.9 kg and 48 cm, 2.5 kg and 57 cm and 2.7 kg and 55 cm.

Growth rates

Twenty-nine pups were recaptured after intervals of 34 days or longer (mean interval = 65.7 days, SD = 11.9, range (34-98). Male growth rates (mean = 95 g/day, SD = 15 g, range = 67 - 123, N = 18) were faster than female growth rates (mean = 83 g/day, SD = 10 g, range = 63 - 88, N = 11) (Fig. 9.2; Mann-Whitney U-test: U = 149,49; N = 18,11; P .03).

Fourteen pups were recaptured after intervals of 11-28 days. As would be expected, rates were much more variable than those observed for the longer intervals: males mean = 79 g/day, SD = 33 g, range = 41 - 132 g, N = 6; females mean

= 72 g/day, SD = 34 g, range = 39 - 132 g, N = 8. A female and a male pup both achieved the maximum growth rate observed in this study by gaining 3.2 kg in 24 days.

Small pups appeared to grow at approximately the same rates as large pups (Table 9.1). The five smallest pups gained on average 92 g/day, whereas, the 6 largest pups averaged 93 g/day.

TABLE 9.1 - Comparison of growth rates for large vs. small pups.

	SEX	WT.(kg) 1st CAPTURE	WT. (kg) 2nd CAPTURE	INTERVAL (DAYS)	GROWTH RATE (g/d)
	M	1.8	7.7	62	95
SMALL	F	2.4	8.4	68	88
PUPS	F	3.2	8.4	67	78
	M	3.6	11.1	65	115
	F	3.6	9.8	71	86
	MEANS	2.9	9.1	67	92
	M	5.9	11.3	63	86
	M	5.9	10.9	51	98
LARGE	F	5.9	11.8	68	87
PUPS	M	6.8	12.0	51	102
	M	6.8	14.5	74	104
	F	6.8	14.1	88	83
	MEANS	6.4	12.4	66	93

Timing of parturition

The modal estimated birth date for Prince William Sound pups was between May 20 and May 29 (Fig. 9.3). Male and female pups were born in nearly constant proportions throughout the spring. The rapid increase in births after April 30, and decrease after June 28, is a conspicuous characteristic of the distribution. It is widely accepted that the timing of the seasonal peak in birth rates varies seasonally throughout the sea otter's range, but that pups are born in all seasons. The spring abundance of young sea otters is readily observable in the Prince William Sound, and elsewhere. However, since pups were caught only between early June and late September, it could be argued that the apparent rapid changes in birth rate were an artifact of the sampling scheme. A perceived late April increase could result if large pups, those born in April or earlier, were present in June, but were too large to be captured in a dip net. In fact, capture success does tend to be lower for pups that are larger than about 10 kg. However, relatively large pups were

captured. Seventy-three pups weighing at least 9.1 kg (20 lb) and 10 pups of at least 13.6 kg (30 lb) were dip-netted. If pups were commonly born in early April, they should have been obvious and easily captured since they would have weighed only 8-10 kg by the end of June. However, at that time of year pups of that size were seldom observed. The pups dip-netted in June (N = 44) weighed on average 4.9 kg (10.9 lb) with the largest being only 8.6 kg (19 lb).

Few pups were born during the mid and late summer. Given the intensity of capture effort after August 28 (N = 50), quite a few small pups should have been captured if they were in the study area in the late summer and early fall. Data on 22 pups, dip-netted between 21 and 30 September, 1986, support the contention that pups were rarely born after June in the Prince William Sound. The average pup captured during this interval weighed 10.4 kg (22.8 lb). The smallest pup captured weighed 5.2 kg, a value heavier than the average weight of June pups.

Incorrect assumptions about growth rates could cause errors in calculations. Moreover, such errors would be greatest for individuals that were not caught until they were fairly large. In order to illustrate the potential magnitude of such errors, we calculated the difference between the estimated birth dates of individuals under two assumptions about growth rates. That is, we made two separate calculations: the first using a growth rate of + 1 standard deviation (SD) and the second using - 1 SD (Table 9.2). Since it was noted that pups caught before August 1 tended to be smaller than those caught afterward, data were displayed accordingly. For example, male pups born before August 1 weighed, on average, 5.7 kg. If a growth rate of 82 kg/day (-1 SD) was assumed, and the real growth rate was 95 g/day, the estimated age of one sixth of the male pups, when captured, would have been at least 6.6 days greater than it really was. Likewise, if the growth rate was assumed to be 109 g/day (+1 SD) the estimated age of one sixth of the males would have been at least 4.8 days less than their real age. Calculations on pups caught after August 1 tended to have a greater error potential, since the pups were larger. Conversely, calculations on females had less error potential since females were smaller and had slower growth rates.

Progeny sex ratio

Sex was determined for 156 dependent pups (Table 9.3). Total sex ratio favored males, but not significantly so. Substantial differences in sample sizes and proportions existed between years so a yearly average was also calculated. This average favored females, slightly. Additional data on

TABLE 9.2 - Error in estimation of birth dates from growth rate assumptions.

	CAPT. DATE	AVE WT (kg)	ASSUMED GROWTH RATE -SD	AVE	+SD	DEVIATION FROM EST. AGE -SD	+SD
MALES	EARLY	5.7	82	95	109	+6.6	-4.8
	LATE	9.6				+13.2	-9.8
FEMALES	EARLY	5.6	77	86	95	+4.8	-4.5
	LATE	9.0				+9.5	-7.7

22 dependent pups near False Pass, on the Alaska Peninsula, included 14 males and 10 females. Thus, the observed total sex ratio, for dependent pups from 2 populations was 95:85.

Dependency period

We assumed that pups were weaned at the time they become separated from the mothers. This follows from the observations of Schneider (1978b) who found that "...females with even the largest pup were found to be lactating." and Payne and Jameson (1984). The peak time of maternal separation for 21 pups that were instrumented during 1985 was October 16 - November 15 (Fig. 9.4). The study otters were not monitored between December 15, 1985 and February 8, 1986. The fact that three pups were weaned during this interval is reflected on Fig. 9.4.

The chronology of the dependency periods of radio-implanted pups is given (Fig. 9.5). Twenty-seven pups are represented; 6 from 1984 and 21 from 1985. Other pups were monitored during 1984 but monitoring was inadequate during the fall and winter to determine relatively accurate weaning dates. Estimated birth dates for individuals with known growth rates are displayed as unbracketed open circles.

TABLE 9.3 - Sex of dependent Prince William Sound sea otter pups.

	1984		1985		1986	
	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE
EASTERN PWS	34	36	19	10	08	14
GREEN ISLAND	--	--	20	15	--	--
TOTAL	34	36	39	25	08	14
GRAND TOTAL			81	75		
TOTAL PROPORTIONS			.519	.481		
AVERAGE PROPORTIONS			.486	.514		

FIGURE 9.2 -- Growth rates of dependent male and female sea otter pups based on two weighings at least 30 days apart. Males grew faster than females.

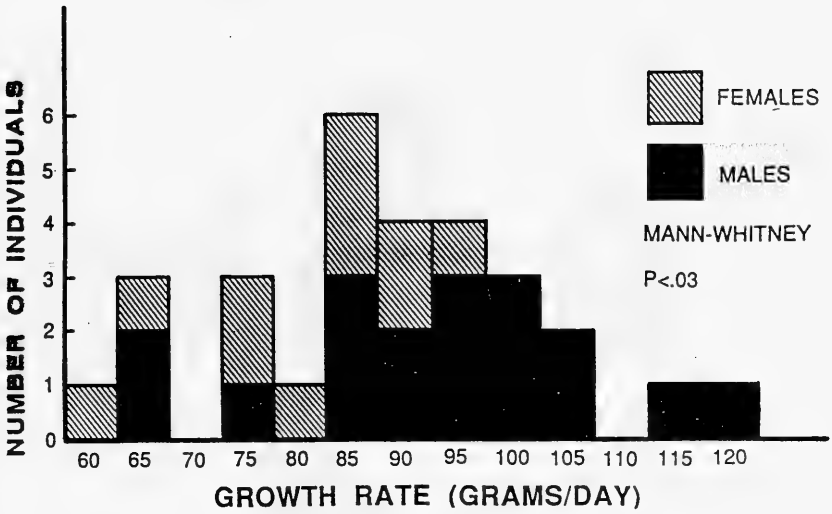


FIGURE 9.3 -- Estimated birth dates and capture dates of sea otter pups in Prince William Sound, Alaska. No tendency was found for one sex to be born earlier than the other.

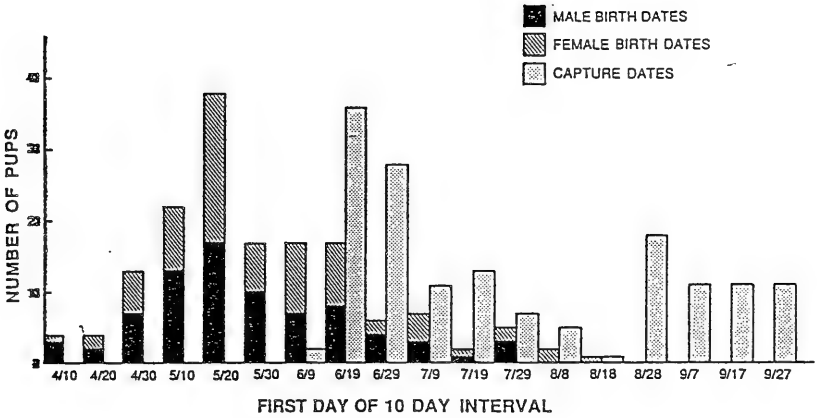


FIGURE 9.4 -- Weaning dates of instrumented sea otter pups in Prince William Sound, Alaska, 1985-1986. Pups were considered weaned when they separated from their mothers. No tendency existed for either sex to be weaned earlier than the other.

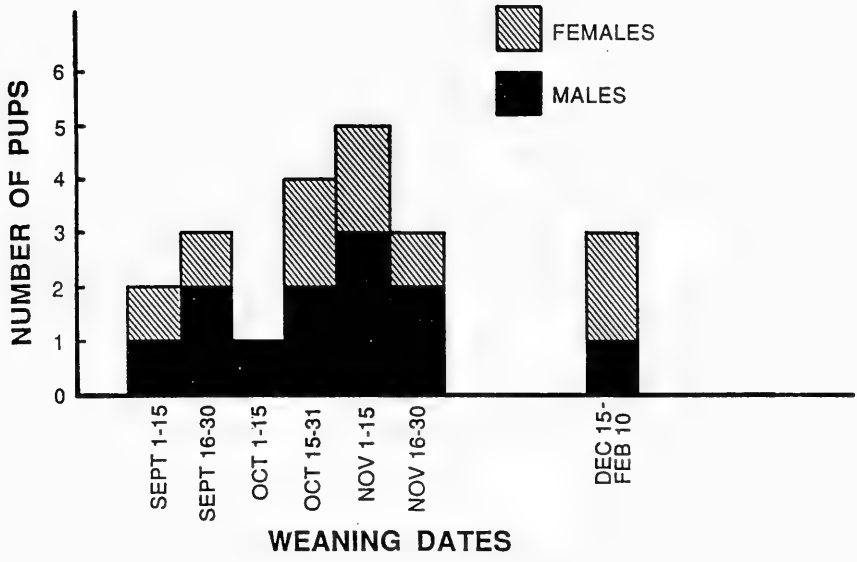
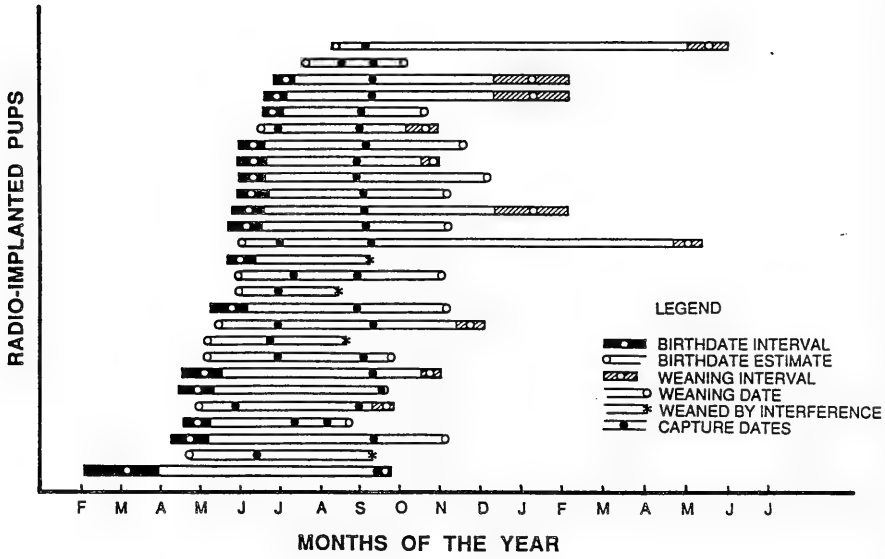


FIGURE 9.5 -- Chronology of dependency periods of 27 sea otter pups in Prince William Sound, Alaska, 1984-1986. Horizontal bars represent individual pups. The main events during dependency are signified by symbols.



When weaning dates were known within plus or minus 4 days they are also displayed as open circles. When dates were less certain, they are displayed as intervals; the intervals being the time between the last sighting before separation and the first sighting afterwards. Four pups were weaned as a direct result of research activities. They are not included in the summary statistics but are considered separately.

The average duration of dependency was 169 days (5.6 months). The range was 76 - 333 days (N = 23). Males did not differ from females (12 males: 170.1 days, SD = 62, 11 females: 167.6 days, SD = 45.6).

Size at weaning was estimated, assuming that growth rates remained constant until weaning. Two individuals that were weaned after 276 and 333 days, respectively, were excluded from this analysis because growth rates could not remain constant for that duration. Males were weaned at a slightly larger size than females (16.2 kg vs. 15.2 kg.). These estimated weaning weights seem reasonable and are consistent with field observations, since large dependent pups are not uncommon. Ten dependent pups were caught in September, or earlier, that weighed between 13.6 kg and 20.0 kg.

The histories of several individuals are remarkable and illustrate the ability of young sea otters to survive even if weaned at very young ages. These are presented as case histories:

Case 1. A male pup was weaned, apparently under normal circumstances, at about 76 days of age and weighing approximately 12 kg. It survived until it drowned in a gill net 9 months later. Both this pup and his mother were instrumented. Thus, the individuals' histories were fairly well known: The mother weaned her previous pup between May 3rd and June 3rd, 1985. She was alone when observed on June 3rd. Although her location was determined several times by telemetry, she was not observed again until August 18, when she was observed accompanied by this male pup. The pup was caught the same day and weighed 5.7 kg. On September 11, 24 days later, it weighed 8.8 kg and was implanted with a radio-transmitter. It was weaned between October 1 and October 10. Based on a measured growth rate of 132 g/day, its birth date was estimated to be 76 days prior to weaning. The maximum possible dependency period, assuming that the pup was born the last day the female was seen unaccompanied and that the pup was weaned the first day it was seen alone, would be 129 days. However, assuming a birth weight of 2.04 kg, this would require a growth rate of 48 g/day. The slowest growth rate observed for a male pup was 67 g/day. If the pup was actually weaned on the first day it was seen alone, the pup would have to had traveled about 50 km on the day it was

weaned, which was possible but unlikely. Thus, this male pup was probably weaned at considerably less than 129 days and possibly at 76 days of age.

Case 2. A female pup was weaned on August 14 when its mother left the vicinity with a male while the pup was undergoing surgery to implant a radio-transmitter. When weaned, it was estimated to be 76 days old. It weighed 9.5 kg. This pup had been previously captured on June 29, when it weighed 5 kg. Thus, based on a measured growth rate of 95 g/day, it was assumed to have been born on May 30. When it was released following the surgery, the pup swam several km across a bay and took up residence in a small, protected cove. It was known to have remained within a km of that site until its radio expired, approximately 20 months later.

Cases 3 and 4. Two pups were weaned during the early fall at under 100 days of age as a result of separation from their mothers during surgery. They weighed 10.4 kg and 12.0 kg when weaned. One, the 10.4 kg animal, died over 4 months later of unknown cause. The other was apparently killed as an incidental take in the local salmon fishery the following June.

Mortality

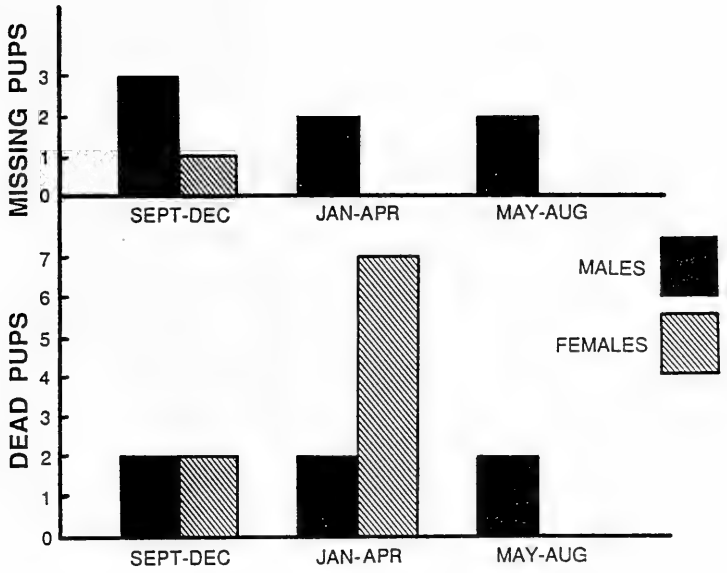
Of the 36 pups that were released with radio-implants, 15 are known to have died and contact was lost with 8 during the life of the study (Fig. 9.6). One of the deaths occurred during dependency and 14 occurred following weaning.

Deaths were most common during the January-April interval, but did occur during all seasons of the year. It was difficult to ascertain the cause of most of the deaths, since beach-cast carcasses were rapidly consumed by bald eagles and other scavengers. However, starvation and predation were both observed and may have been significant during the fall and winter months.

It was apparent that one female starved to death. Her carcass was recovered very shortly after death. At that time she weighed 26% less than she had when implanted, 37 days earlier.

A recently weaned female was killed by coyotes (Canis latrans) in Olsen Bay, at the back of a long tidal flat. It is possible that she became trapped by the falling tide. Her radio was found in newly fallen snow with fresh blood and coyote urine markings. The blood was bright red indicating that it was well oxygenated and thus, that she was killed, rather than scavenged. Three other weanlings were probably killed by coyotes in a nearby tidal basin, locally referred

FIGURE 9.6 -- Sea otter pups instrumented in Prince William Sound, Alaska, that died or with which radio contact was lost. Contact was more frequently lost with males than females. Females tended to die during the January-April interval whereas male deaths were distributed year around.



to as Hell's Hole. All died within a few hundred meters of each other. The first of these weanlings to die had been seen hauling-out on a bank that was heavily used by coyotes, judging from the numerous fresh tracks in the snow cover. This weanling was dead within a week, leaving no traces except the radio on the beach within 100 m of the haul out site. The second weanling's radio was recovered on a nearby beach 2 months later. On the same day, the third weanling was observed alive a few hundred meters away. It had become stranded on an exposed mussel bed, by the out going tide, several hundred meters from deep water. During the next survey, 3 months later, its radio was recovered at the same location as the second weanling's. The radios of several other weanlings were found on large tidal flats. It is conceivable that those individuals became stranded and were preyed upon. Other radios were recovered from rocky beaches in areas subject to wave action. Otters were not observed to haul out at these locations. Thus, it is probable that they died elsewhere, remained intact, and floated to those sites.

Entanglement in commercial fishing gear was a significant problem and a cause of deaths to the sea otters in this study. Commercial fishing is permitted in the general area from May until October. All four of the males that were dead or missing during the May-June interval may have been killed in the fishery. One male's flipper tags were turned in by a fisherman who stated that it had drowned in his gill net. Another weanling was missing a few days after the annual fishing opener, in May. For the preceding 5 months it had occupied an area that was heavily fished during the opener. Presumably, it died and its carcass drifted beyond the study search area. A third male's radio and remains were recovered a few km down current from the same area during the middle of the fishing season. A fourth male became missing near Valdez following an unusually heavy period of gillnetting in the area where he was last seen.

Three other study otters, one an adult female, became entangled in fishing nets but were released unharmed. Three fishermen reported that otters had snagged their button tags on the strands of the net. In one case it was thought that the weanling drowned because it snagged near the bottom of the net and could not surface. It is not possible to say what the role of the tags was in the deaths of these animals. Button tags are no longer used at this study site. It would seem prudent not to use button tags at any location where there is a chance that otters may encounter commercial fishing gear. This includes gill nets, seines, trawls or crab pots.

Radio contact was lost with male weanlings more frequently than it was lost with female weanlings (7:1). It is possible that radio contact was lost because those

individuals left the study area. In this study male sea otter weanlings did travel more extensively than their female counterparts following weaning (Chapter 8). Several of the missing males were last seen near the edge of the study area after traveling as far as 123 km.

Survival and juvenile movements.--The difference in the fates of individuals was striking depending upon whether they were travelers or not. Approximately 90% (28 of 31) of the known or suspected weaning locations were located in three Bays: Sheep Bay, Simpson Bay or Port Gravina. Of the 12 weanlings that remained in those bays: 2 survived, 1 was missing and 9 died. Of the 16 weanlings that left those areas: 9 survived, 4 were missing and 3 died. Even if it is assumed that the missing individuals died, which biases the data against a difference in outcome, survival was lower for weanlings that remained in the weaning areas (Chi square = 3.93, 1 DF, $p < .05$). If the same comparison is made, considering only survival until spring, the relationship is stronger (Chi square = 8.18, 1 DF, $p < .05$). If it is assumed that the missing weanlings did not die, the relationship is stronger since 4 of 5 missing weanlings were travelers. The argument is also strengthened by the fact that the 3 weanlings that were known to have been weaned in bays other than Sheep, Simpson or Port Gravina all survived. Individuals that stayed in the latter bays appeared to be dying mostly of predation or starvation during the fall or winter. However, those that left the weaning areas died mostly in the spring and summer due to human-related activities.

Survival rates

Two sets of survival-related calculations are given (Table 9.4). Sea otters that died of all causes are included in one set. In the second set, deaths caused by human activities are treated as transmitter failures. That is, the otter days are included but the death is not. Mortality that was probably related to the fishery was quite high during this project. Such deaths may be rare in other areas. It is hoped that the alternate sets of calculations will make the data more general.

The only pup to die during dependency was a male pup that died after being hit by a boat propeller. Thus, the survival rate for dependent pups is 1.0 when human caused deaths are not considered but is slightly lower when they are. When the boat strike was included, the survival rate for dependent males seemed low at 0.70. It is, perhaps, more insightful to consider that 20 of 21 (95%) male pups survived the average of 48 days between being instrumented and being weaned. All females (N = 15) survived the comparable period.

TABLE 9.4 - Survival rates of sea otter pups in Prince William Sound.

	ALL MORTALITY				NON-HUMAN MORT.			
	FEMALES		MALES		FEMALES		MALES	
	DAY	YR	DAY	YR	DAY	YR	DAY	YR
DEPENDENT PUPS								
	1.0	1.0	.9990	.70	1.0	1.0	1.0	1.0
	(657)		(1012)		(657)		(1012)	
INDEPENDENT JUVENILES								
ASSUMP. 1	.9969	.32	.9982	.51	.9969	.32	.9989	.70
	(2917)		(2721)		(2917)		(2721)	
ASSUMP. 2	.9966	.29	.9923	.20	.9966	.29	.9966	.30
	(2917)		(2721)		(2917)		(2721)	
ASSUMP. 3	.9974	.38	.9982	.52	.9974	.38	.9989	.68
	(3410)		(2815)		(3410)		(2815)	
ASSUMP. 4	.9971	.34	.9957	.21	.9971	.34	.9974	.38
	(3410)		(2815)		(3410)		(2815)	

* Numbers in parentheses are "otter days".

ASSUMPTIONS:

Weaned 1: Died day of last sighting, missing pups are alive.

Weaned 2: Died day of last sighting, missing pups are dead.

Weaned 3: Died day carcass found, missing pups are alive.

Weaned 4: Died day carcass found, missing pups are dead

The survival rates of weanlings are lower than those of dependent pups. Female rates are the least variable, ranging from 0.29 - 0.38 depending upon assumptions made in calculations. The exclusion of human-caused deaths has no effect on rates since no females died as a result of the fishery. As noted, females were caught in fishing gear, but all were released. Male survival rates are quite variable, 0.21 - 0.70, depending upon the assumptions made in calculations and whether human-caused deaths are included. Changes in frequency of monitoring had little effect. However, potential mistakes in determining weanling survival (i.e. incorrect assumptions about the status of missing individuals) could lead to a change in survival rates by a factor of 2.

DISCUSSION

The results of this study indicated that there exists substantial variation in the timing of births, growth rates and dependency periods between individual sea otters. Males

grew more rapidly than females, were weaned at slightly heavier weights and thus, apparently required more parental resources (i.e. food) than did females. However, male and female births were timed similarly, and dependency periods were of approximately equal duration.

Data indicated that young sea otters were capable of surviving independently long before they reach the typical age of weaning (i.e. approximately 5-6 months), even when they were weaned prematurely by human interference. In general, however, weanling survival rates were low during the first year of independence. Male weanlings were more likely to survive their first year of independence than were female weanlings. Observed differences between male and female weanlings in rate and timing of mortality existed and appeared to be strongly related to whether weanlings established their post-weaning home range in male areas or female areas.

These data offer some support for the body of theory that suggests that sea otters should make a larger parental investment in male offspring.

PI and growth rates

The faster growth exhibited by males suggests that females may allocate more resources to dependent sons than to dependent daughters. Based on the arguments of Trivers and Willard (1973), it is possible that only the females that can best do so, produce males. Such females might be those that were older, larger or more experienced. This hypothesis requires the implicit assumption that there exists some mechanism whereby these individuals would tend to conceive sons, or possibly abort females (see Clutton-Brock and Albon, 1982, for a discussion of such mechanisms). Substantial variation in pup sex ratios was observed in this study, but it is not possible to say whether such variation was related to maternal factors in any systematic way.

Another way in which a female could allocate more resources to a son would be trade off future reproductive potential in order to produce an adequate male, once one is conceived (reviewed in Clutton-Brock and Albon, 1982). The faster growth of sea otter males during dependency suggests that male pups may require greater investment from their mothers than do female pups. It seems unlikely that males assimilate nutrients more effectively than females, since growth rates of male mammals are usually more strongly affected by food shortages than those of females (Widdowson, 1976). Unless food is unlimited, a male's greater need for milk or solid food could negatively affect its mother's health, both by affecting her overall condition and/or by causing imbalances of critical elements at the time of

weaning. These "costs" to the mother could be manifested in effects on future reproductive potential through, for example, skipped or aborted pregnancies and reduced life span. It is possible that such "costs" exist for females that produce sons, especially if they live in habitats that have been heavily exploited. For example, higher rates of *in utero* mortality and lower overall rates of reproduction have been observed in sea otter populations that have over-exploited their food supplies (Schneider 1978b; reviewed in Simon-Jackson and Rotterman 1987).

Timing of parturition

Other information on sex differences in birth dates is not available. However, the observed late May peak of pupping is consistent with observations from other locations within Alaska. Barbash-Nikiforov, et al. (1978) observed a peak during May-June in the western Pacific. Schneider (1978b) reported a May peak in the central and western Aleutian Islands.

Dependency period

Dependency period lengths were quite variable for pups in this study and for pups in other studies at different locations throughout the sea otter's range. Data from research carried out along the eastern coast of the Soviet Union (Barabash-Nikiforov, et al., 1978), and in the western and central Aleutian Islands (Kenyon, 1969; Schneider, 1978b) suggested that females in some populations nursed pups for approximately one year. Other studies in Alaska and California have reported dependency periods averaging 5-7 months (Garshelis, et al., 1984; Wendell, et al., 1984; Payne and Jameson, 1984). Dependency periods in this study ranged from 2.5-11 months.

Several variables might contribute to variation in dependency periods. The underlying food supply could affect dependency periods both by influencing the development of young animals directly, and by affecting them indirectly through the mother. It is likely that pups must reach a minimum size and minimum level of experience to be able to survive, in a given environment, upon independence. Food abundance should affect growth rates and, hence, the time it takes to reach that minimum size. If food was abundant, shorter dependency periods could result. Also, food abundance might affect the minimum size and experience requirements. If food was abundant, less precocious weanlings might be able to feed more effectively, mistakes would be less critical and thus, pups could be weaned earlier. If females were in good condition, they might be able to raise a pup more quickly or,

conversely, better afford to continue to support one. The same might be true for older, more experienced, females.

Sex ratio

No data are available from this study that would give any insight into the reason for the variation in pup sex ratio that was observed. However, a number of maternal or environmental factors are believed to be correlated with biased offspring sex ratios in mammals. These include: maternal age, parity, reproductive history, dominance status, size or nutrition and birthdate, litter size or timing of conception. Recent reviews of these factors, and relevant theories, are available in Clutton-Brock and Albon (1982) or Clutton-Brock and Iason (1986).

The only data that are available on the sex ratio of young sea otters, other than this study, are from Amchitka during the 1960's (Kenyon 1969). Kenyon (p. 206) reported that the sex composition of 117 recently "deserted" or dependent "juveniles" (individuals of less than one year of age) was 58 males, 58 females, and one unknown. Schneider (1978b) and Kenyon (1969) reported fetal sex ratios from studies in the central and western Aleutian Islands. Combining their data, of 319 fetuses, 171 (57%) were females and 138 (43% males).

Survival rates and causes of mortality

Parental investment theory suggests that sex differences in post-weaning behavior, especially movement patterns, could lead to male and female offspring being subjected to different risks. Different selection pressures could, in turn, lead to different mortality patterns. Mortality rates and patterns were different for male and female sea otter offspring. Unexpectedly, females (the nondispersing sex) exhibited lower survival rates, during the first year after weaning, than did males. The trend toward a higher rate of male post-weaning survival in this study was similar to the trend in juvenile survival in California (Chapter 2).

Comprehensive discussions of causes of sea otter mortality are available elsewhere for California (Riedman, 1986) and Alaska (Kenyon, 1969; Simon-Jackson and Rotterman, 1987). These include: starvation, disease, parasitism, predation, shark attacks, accidents during research projects, entanglement in fishing gear, adverse weather conditions (storms and icing), boat strikes, and injuries received from conspecifics during fighting or mating.

The results of questionnaires (Simon-Jackson, 1985) and surveys (Matkin and Fay, 1980; Simon-Jackson, 1986) have

indicated that there is a significant mortality of sea otters, incidental to the salmon fishery in Prince William Sound and on the nearby Copper River Delta. Incidental take of sea otters in commercial fisheries is not unique to, but is especially significant in the Cordova vicinity (Simon-Jackson, 1986; and reviewed in Simon-Jackson and Rotterman, 1987). Sea otter encounters with fishing gear are frequent and increasing on the Copper River delta and within the Prince William Sound. It is known that many untagged otters have died in fishing gear, either from drowning or from fishermen killing them directly.

Why is first winter survival high in the male area?

The male area is mostly contained within shallow, protected channels within estuarine mud flats that contain abundant shellfish species. Such habitat is scarce in the weaning areas. Food was considered to be abundant in the local male area when otters first recolonized it (Garshelis, et al., 1986) and apparently still is. Otters in the male area are frequently killed by natives, fishermen, and others. In such cases, recovered carcasses were examined and found to have significant subcutaneous fat. Moreover, stomachs usually contained large quantities of clam and/or crab tissues (pers. obs.). In addition to abundant food, the local male area offers young otters other benefits. There are large aggregations of males of all ages, so opportunities for learning from adults also exists (Garshelis, et al., 1984). Moreover, large predator-free, sand bars are exposed at moderate tides. These are heavily used as haul-out areas, especially during the winter. The energetic advantages of such behavior in cold water environments could be substantial.

Why are pups weaned in bays where they are likely to die?

Some weanlings apparently died of starvation during the first few months after weaning. The apparent maladaptive practice, of females weaning pups in areas where they have little chance of over-winter survival, may be a consequence of changing, conflicting needs during the development of the pup. On one hand, the deep, protected northern bays offer shelter and abundant pup food in the blue mussels (Mytilus edulis) which cling to the steep rock walls and grow in dense beds in the shallows. Opportunities exist for pups to learn self feeding in protected channels and lagoons. On the other hand, these bays tend to be deep and steep-sided so other larger prey may be relatively unattainable to small, newly independent otters whose diving abilities are usually limited. Although it seems probable that small juveniles can survive on a diet of mussels alone, it is not clear whether large juveniles can.

Predation appears to be a significant source of mortality of young sea otters in the weaning areas. Moreover, the rate of predation could be exacerbated by juveniles' tendency to haul out when subject to food stress, as would occur under the preceding argument. Predation on hauled sea otters has not been noted before this study and may be uncommon. If so, it would be unlikely that adult sea otters would be prepared to respond to the possibility when choosing sites for weaning pups.

Recolonization and future changes

The Prince William Sound sea otter population is still recovering from near extirpation, which took place at the end of the 18th century (Lensink, 1962). The bays in which weaning was observed in this study, Simpson Bay, Sheep Bay and Port Gravina, were reoccupied by large rafts of males between 1970-1979 (Garshelis, et al., 1986).

While it is risky to predict the patterns that will develop for otters in this area when the population approaches equilibrium, a few speculations can be made. It is likely that food resources in the three bays have been depressed as a result of the relatively recent occupancy by large rafts of males (Garshelis, et al., 1986). However, it is possible that food levels will eventually rise above current levels, after the population reaches equilibrium (e.g. Estes, et al., 1978; Estes, et al., 1982). If food levels do rise, juvenile starvation may decrease in those bays. Moreover, deaths from predation may also decrease. Predation can occur when individuals haul out on beaches. Moribund sea otters usually haul out (Kenyon 1969), which would be the case if food was scarce and they were starving. Thus, if food became more abundant the frequency of hauling-out and, hence, predation might decline. Conversely, it might be predicted that food abundance in the male area will decline, at least initially, after a longer period of sea otter occupancy. If so, starvation would increase. Predation, however, might remain unaffected since numerous safe haul out sites are available on sand bars in that area.

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CHAPTER 10

A SIMULATION MODEL FOR ASSESSING THE RISKS OF OIL SPILLS TO THE CALIFORNIA SEA OTTER POPULATION AND AN ANALYSIS OF THE HISTORICAL GROWTH OF THE POPULATION

A. BRODY

NOVEMBER 30, 1988

INTRODUCTION

The model described in this chapter is designed to facilitate analysis of the risk of oil spills to the California sea otter population. Specifically, we provide a simulation of aspects of otter population biology and behavior that will likely affect the degree of risk to the population associated with oil spills. We have not conducted actual risk analysis with the model.

Ford, et al., (1982) describe two general categories of oil spill consequences that affect the degree of risk of oil development activities to a wildlife population: 1) immediate mortality from a given oil spill, and, 2) long term population effects. Our model addresses the first category explicitly, and can be used to address the second category if the long term effects of oil development are assumed to result only from mortality due to oil spills. Our model was formulated to answer two specific questions about a given oil spill: 1) how many otters will be killed, and 2) how long will it take for the population to recover.

General approach

There is a good deal of uncertainty surrounding certain aspects of sea otter ecology in California, and a general lack of data regarding most aspects of the population dynamics. There are also ongoing research projects being conducted by various agencies and organizations aimed at correcting these situations. A major objective in structuring our model was that it be flexible enough to explore a variety of conceptual hypotheses about sea otter ecology, and to incorporate new data as they become available.

As with any simulation model, some simplifying assumptions about the system are necessary. Four major ones will be discussed in this introductory part of this chapter, others will be mentioned at appropriate places later on.

1) Geometry of sea otter range.-- The sea otter range in California is essentially linear, consisting of an approximately 350 km long by 1 km wide band along the coast. The width of the range is dictated by the slope of the ocean floor, with otters generally inhabiting only areas shallower than 18m (USFWS 1986); in some areas of the coast the 18m depth contour is more than 1 kilometer offshore, and animals may occasionally be found at locations of deeper depth. In fact, telemetry data gathered as part of this project indicates that certain segments of the population may utilize offshore areas more frequently than previously realized (see Chapter 3). But in the model we consider the range to be one dimensional, a line extending up and down the coast.

California Department of Fish and Game has traditionally used the "as the otter swims line" (Ames, Hardy and Wendell, personal communication), an ordinate system coincident with the 5 fathom (10m) depth contour, in their census activities. With an origin at Coyote Point on the San Francisco peninsula, position along the coast is measured in 500m units south of the origin. We have adopted this system for the spatial aspects of our model. This system allows us to incorporate existing census data, to ignore the shape of an oil spill and be concerned only with the length of coast affected, and to facilitate the analysis and modeling of sea otter movement.

2) Density dependence in population dynamics.--A good deal of controversy surrounds the role of density dependence and the question of non-equilibrium in the current theories of population dynamics. The issue is complicated by the range expansion that has accompanied population growth, differences in habitat quality at various locations within established and potential range, and the role of the sea otter as a "keystone species", able to dramatically affect the quality of its own habitat (Miller 1980, Estes, et al., 1982, Estes, et al., 1986, Wendell, et al., 1986). Rather than assume density dependent or density independent dynamics, we have built in a flexibility that allows investigation of both. The population dynamics portion of our model nominally assumes density dependent growth during recovery from an oil spill. The equilibrium population size and a parameter governing the shape of the density dependence function are easily manipulated at the beginning of a model run, however, and density-independent population growth can be simulated by setting parameter values that result in an essentially flat density dependence function.

3) Range expansion.--Related to range geometry and the nature of population dynamics is the question of range expansion. It is an especially critical question given the purpose of the model, as the offshore areas most likely to be developed for oil and gas in the future are at the southern periphery of the existing sea otter range (USFWS, 1986). Thus, if we are to make reliable predictions about the effects of oil spills very far into the future we must be able to make predictions about the extent of sea otter range in the future. Unfortunately, data collected during this study do not easily lead to such predictions. We assume in the simulation model that the extent of the range is static, and that otters distribute themselves along the coast in the same relative proportions regardless of total population size. We have, however, built a separate, small, deterministic model that will generate predictions of future range length, carrying capacity, and population size based on historical rates of population growth and range expansion. This model, OTRANGE, described elsewhere in this report, can be used to generate

range conditions for use in the population model. It only applies to the existing sea otter range in California and does not extend to the translocation of otters to San Nicholas Island.

4) Impact criteria.--In line with the stated purpose of the model, three criteria are assumed to measure the effect of an oil spill on the population. The first criterion is the number of animals and proportion of the population killed by the spill. The second criterion is the number of years after the spill that is required for the population to recover to pre-spill size. The third criterion is the decrease in the total reproductive value of the population (Wilson and Bossert 1971), providing a measure of how the perturbation in age and sex structure caused by an oil spill may affect population dynamics. This is calculated using the survival and reproduction rates operative in the population just prior to the spill, before density dependent adjustments to these rates are effected. In addition to these three criteria the model can be run in a "control" mode, in which an oil spill is not introduced, allowing graphic comparison of population dynamics with and without perturbation by oil spill.

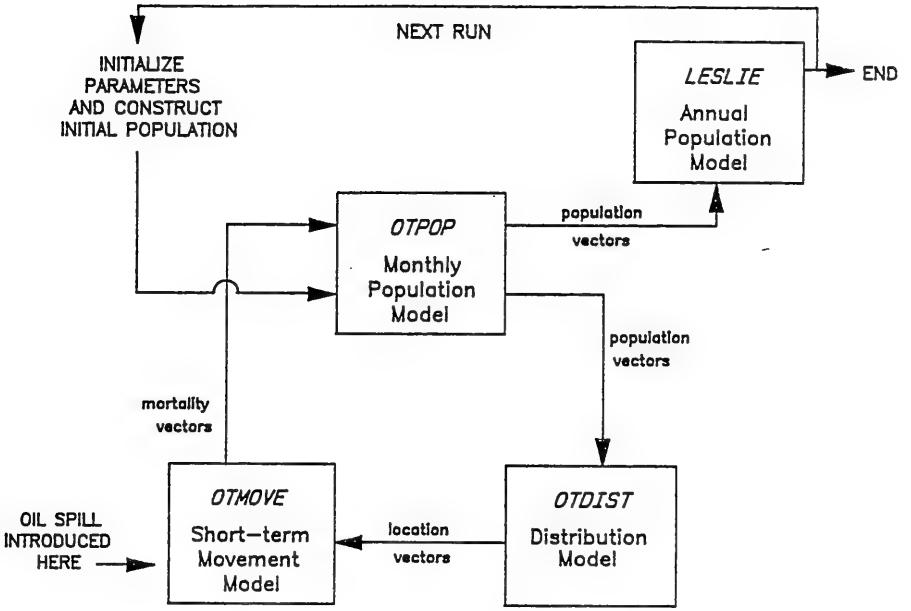
Model structure

We model the effect of an oil spill on the sea otter population as being determined by the size and location of the spill in relation to sea otter distribution, the movement of individual sea otters in the vicinity of the spill, and sea otter population dynamics.

The model itself consists of four submodels imbedded into a larger program superstructure (Fig. 10.1). The submodels, all of which are stochastic, operate in different temporal and spatial scales. The short term population submodel (OTPOP) operates with a time step of one month and is spatially independent. The long term population model (LESLIE) operates on an annual time scale and is also spatially independent. The sea otter distribution model (OTDIST) operates on a spatial scale of kilometers, and is time independent. The short term movement and oil response model (OTMOVE) operates with a time step of days, and on a spatial scale of kilometers. Each of the submodels operates on a numerical scale of individual animals.

OTPOP creates a simulated initial population, and iterates for three simulated years before an oil spill. In the month of the simulated spill, population vectors, consisting of the age and reproductive status of each individual animal in the simulated population, are passed from OTPOP to OTDIST. OTDIST assigns each individual a position

FIGURE 10.1 -- Schematic representation of the interrelation of the 4 submodels used to predict the potential effects of oil spills on California sea otter population dynamics.



along the coast, and passes these vectors to OTMOVE. OTMOVE introduces an oil spill, moves animals along the coast during the duration of the spill, and generates a mortality vector. This mortality vector is then returned to OTPOP, and two years of population recovery are simulated on a monthly basis. At the end of the second year after the simulated spill, the population vectors representing individual animals are collapsed into age class vectors and passed to LESLIE. LESLIE then simulates the future course of population growth on an annual basis for up to 50 years.

While the structure of the model is essentially set, and can be altered only through reprogramming of the source code, the parameters used in the model are set each time the model is run. We have supplied a set of default parameters, representing our best estimates of the values operating in the real population, but these may be altered by the user to investigate the importance or sensitivity of parameters or to take advantage of revised parameter estimates that may be available after future research. Following is a detailed discussion of the structure of each of the submodels, and the logic that we followed in arriving at the default parameter estimates.

OTPOP AND LESLIE

Structure

The small size of the population allows a reasonably efficient consideration of individual animals. The reproductive biology of sea otters, specifically the fact that pupping is spread throughout the year rather than concentrated into a short reproductive season, adds a complexity to the sea otter model that is not present in population models of most other large mammals. OTPOP thus iterates on a monthly basis.

At the beginning of each run the user specifies an initial population size, a carrying capacity for the range, a maximum population growth rate, and a parameter governing the shape of the density dependence (population growth rate vs. population size) curve. The initial growth rate of the population is calculated on the basis of these parameters and used to construct an initial population vector with a stable age distribution.

The age, in months, of each male in the population is stored in a male age vector. The age, in months, of each female in the population is stored in a female age vector. The reproductive status of each female in the female vector is stored in the
corresponding element of a reproductive vector.

During each month of simulation the model loops through each individual in the population, drawing a random number that is compared against age- and sex- specific monthly survival rates to determine whether or not the animal survives the month. In the female loop the reproductive status of each surviving female is checked. If a female has a pup the survival of that pup is determined by drawing a random number and comparing it to monthly pup survival rates. If a female has no pup, she becomes pregnant with probability determined by her age and the month of the year. Inter-uterine mortality is assumed to be zero so that if a pregnant female survives a given month her fetus automatically survives also.

The age of any animal that does not survive the month is flagged. If a pup dies, the mother is assumed to get pregnant again immediately. If a pup survives until weaning it is assigned a sex randomly and added to the appropriate age vector. At the end of each monthly loop through the population the vectors are reloaded without the animals that have died, and numbers are totaled and reported.

The model is allowed to run for three simulated years before an oil spill is introduced, to subject the initial stable age distribution to stochastic fluctuations. In the year of the spill, OTDIST and OTMOVE are called and subject the population vectors to oil spill induced mortality. Oil spill mortality is considered after the regular loop for that month has been completed, but after the population vectors are reloaded. Thus simulated oil spill mortality is strictly additive to the simulated natural mortality.

OTPOP continues to iterate on a monthly basis for two simulated years after the spill, with population growth rates determined by the density dependence function annually. Two years after the spill the population vectors are collapsed into age class vectors and passed to LESLIE. Pups and fetuses are grouped into age class 0, age class 1 contains animals between seven and 18 months of age, age class 2 contains animals between 19 and 30 months, etc. The numbers of animals of each sex in age class 0 are determined by a random draw from a binomial distribution assuming a 0.5 probability of being either sex.

LESLIE, iterating on a yearly basis, runs much faster than OTPOP at the expense of seasonality. Population sizes are reported once a year, at the end of the month in which the oil spill occurred. Survival and reproductive rates based on the density dependence function are determined at each iteration, just as in OTPOP. Two sources of variation, after Harris, et al., (1987), are considered explicitly in LESLIE. The first is a "demographic" stochasticity wherein it is assumed that all animals of the same age and sex have the same

probability of surviving the year, but the number that actually do survive is determined by a random draw from a binomial distribution with parameters (n_x, s_x) where n_x is the number of animals in age class x and s_x is the annual survival rate for age class x. If n_x is greater than 30 the normal approximation to the binomial is used to reduce the computer time required. The second source of variation is "environmental" stochasticity that operates simultaneously across all age classes to the same degree in a given year. This is introduced to simulate the occurrence of "good years" and "bad years". The bounds of this stochasticity are determined by the user at the beginning of the run, and p, the environmental stochasticity parameter, is assumed to be uniformly distributed between those bounds. At the beginning of each simulated year p is determined once by random draw and the survival rate, s_x, of each age class for that year is modified by adding ps_x.

Built in to the structure of LESLIE is the ability to consider density independent mortality. This is included primarily because of the possibility that incidental gill- and trammel-net mortality, which has substantially affected population growth in recent years (Ames, et al., 1985, Wendell, et al., 1985, Estes, et al., 1986) operates in a density independent fashion. The user may set a density independent mortality rate, applied to all age classes, and also the degree to which this density independent mortality compensates for density dependent mortality.

Theoretical framework for parameterization of OTPOP and LESLIE.

Field data that can be used to infer the dynamics of the California sea otter population are scarce. Raw data available to us included aerial and ground censuses conducted by the CDFG and the U.S. Fish and Wildlife Service (1968-1985), records from CDFG and USFWS carcass recovery efforts (1968-present), monthly counts from several CDFG and USFWS index areas (1976-1982), and our own live-capture and telemetry data. In addition to this raw data, information on sea otter population dynamics was gleaned from several publications and manuscripts.

The information available to us differed greatly in reliability, in relative quantity, and in the extent to which it was directly applicable to our purposes. Bringing all of the information together into a single flexible yet comprehensive model required the use of a strong theoretical framework, necessary both for evaluation of the available data and for estimating model parameters. The theoretical framework that we used was developed by Eberhardt (1985)

following work by Siler (1979), and based on the classical age structure models of Lotka (1907).

Survivorship.--Siler (1979) and Eberhardt (1985) viewed survival to any age as a function of three "competing risks". The first risk is that of "early hazards", risks which are associated with the early years of life, but become much less important as the animal matures. In sea otters these early hazards are most likely to be associated with dispersal from the natal area after weaning, and with low competitive ability relative to older, more experienced animals. The early hazards risk is greatest in the first years of life, but essentially zero after maturity. The second competing risk is that of incidental, or "constant hazards", which in sea otters would include those due to possible predation, severe weather, infectious disease, and possibly accidental entanglement in commercial gill and trammel nets. This risk is seen as constant throughout an animal's life, and is the only important risk of mortality during the prime adult years. The last risk is that due to senescence, and in sea otters would include reduced competitive ability or increased susceptibility to disease due to old age. This risk is essentially zero through the prime adult years, but reaches 100% by the maximum age.

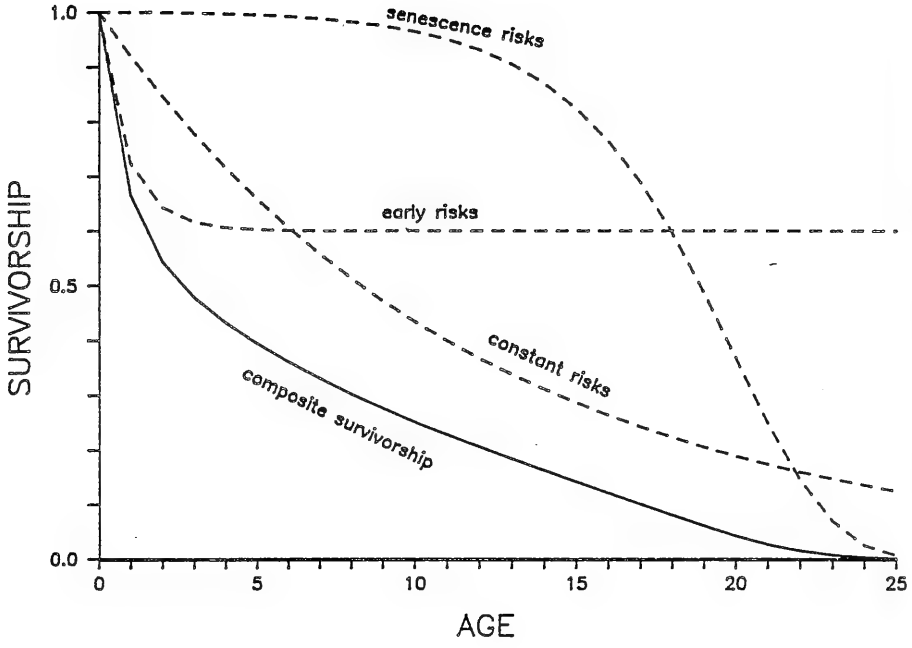
The probability of survival to any age, then, is the probability of surviving all three competing risks at that age, or the product of the three age specific survival rates (Fig. 10.2). Estimating the survivorship schedule inside of this framework allows calculation of survival rate for each age class without having to estimate each directly from field data. The number of parameters that have to be estimated is thus greatly reduced. Sea otters are long-lived; the data for directly estimating survivorship for perhaps 25 age classes are simply not available. Using Eberhardt's (1985) approach we need only to determine the form of the three competing risk curves.

The equation for survivorship at age x, from Eberhardt (1985) is:

$$l_x = \exp\{-a_1[1-\exp(-b_1x)] - a_2x - a_3[\exp(b_3x)-1]\} \qquad (1)$$

where l_x is survivorship, a_1, a_2, a_3 are the coefficients for early, incidental, and senescence risks, respectively; and b_1, b_3 are parameters governing the shape of the early hazards and senescence curves, respectively. In this formulation the risk coefficients (a_1, a_2, a_3) are taken as $-\ln(S)$ where S is the annual survival rate against early hazards, incidental

FIGURE 10.2 -- Hypothetical survivorship curve depicting the relationships of the 3 competing risks of Siler (1979) and Eberhardt (1985).



hazards, and senescence, respectively. Separate survivorship curves can be generated for males and females using the basic equation with different parameter values.

Reproduction.--As for survivorship, age specific reproduction can be modeled as a function of three component curves: an early reproductive function, a "prime" rate during adulthood, and a decrease in reproductive output during the years of senescence (Fig. 10.3). Again, conceptualizing reproductive rates in this manner greatly reduces the number of parameters to be estimated. If early reproduction increases asymptotically to the prime rate a separate term governing early reproduction is not necessary, and Eberhardt (1985) gives an equation for the reproductive curve:

$$m_x = A\{1-\exp[-b_A(x-C)]\}\exp[-a_3\exp(b_3x)-1] \qquad (2)$$

where m_x is the number of female offspring per year weaned by each female of age x, A is the maximum reproductive rate (in number of female offspring weaned per prime aged female), B is a parameter governing the rate of increase of early reproductive rate to the prime rate, C is the age before the age of first reproduction, and a_3 and b_3 are the senescence parameters as in (1).

Population growth rate and density dependence. The per capita population growth rate is a central parameter in any population model. Recent investigations suggest that in marine mammal populations the dependence of population growth rate on population size is nonlinear, with the growth rate decreasing more and more rapidly as the population approaches carrying capacity (Eberhardt and Siniff 1977, DeMaster 1981, Fowler 1981). We generalized DeMaster's (1981) density-dependent relationship for survivorship to obtain a simple non-linear function for population growth rate:

$$r = r_{max}\{1-\exp[-b(K-N)]\} \qquad (3)$$

where r is the annual per capita growth rate, r_{max} is the maximum annual per capita growth rate, N is the population size, K is the equilibrium population size, and b governs the shape of the curve. Because growth rates determined according to (3) decline unrealistically rapidly when the population size gets very far above the equilibrium level we impose an arbitrary floor on the growth rate at $-r_{max}$ (Fig. 10.4).

Lett, et al., (1981) and Fowler (1981) point out that density dependence in age-structured populations may be

FIGURE 10.3 -- Hypothetical reproductive curve depicting the relationship between prime reproductive rate and senescence, after Eberhardt (1985).

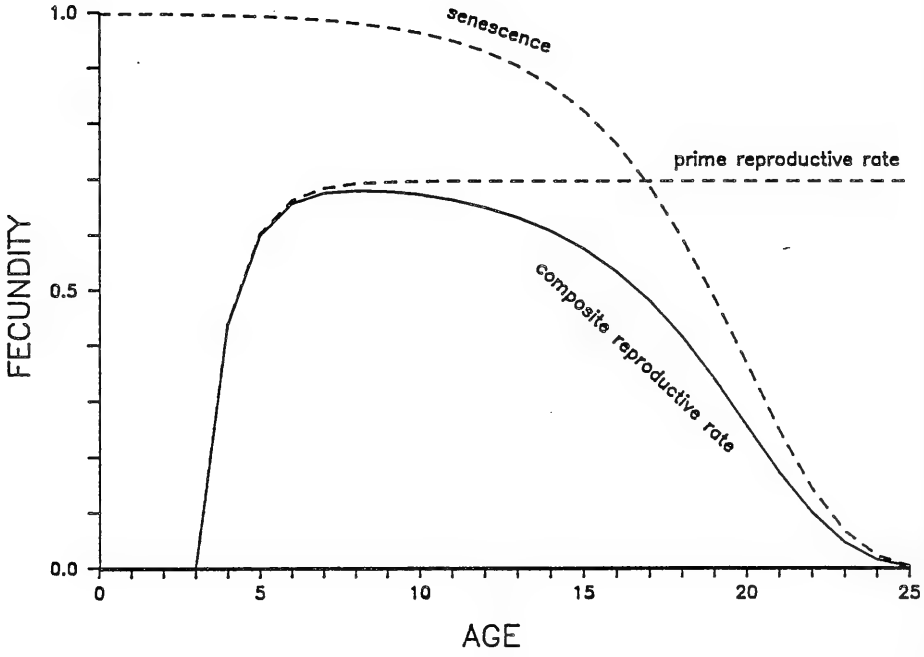
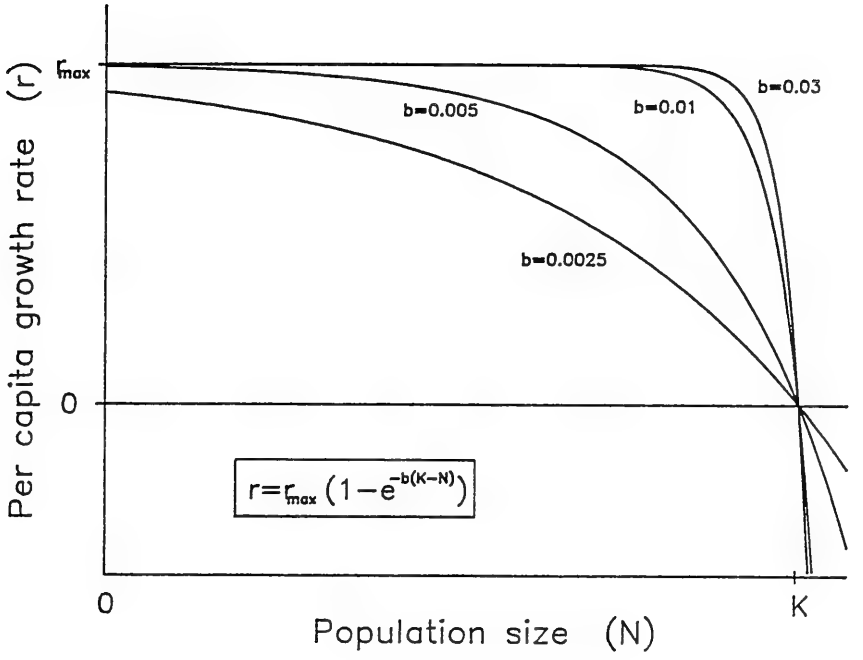


FIGURE 10.4 -- The effect of the value of b on the non-linearity of the density dependence function used in OTPOP and LESLIE. K is the carrying capacity.



mediated through a variety of mechanisms including age at first reproduction, pregnancy rate, age of weaning, juvenile survival rate, and/or adult survival rate. Our California field work indicates that juvenile females are under more intra-specific competition pressure and suffer higher mortality rates than adults. Our model incorporates a hierarchical adjustment mechanism in the calculation of female parameters to achieve the annual growth rates specified by (3). Most density dependence is effected only through changes in the female early risk coefficient (a_1 in (1)); if the early survival rate drops below .40 or rises above the incidental survival rate, the incidental female risk coefficient (a2) is altered. If the incidental survival rate reaches 0.99 (i.e., extremely high values of r), the age at first reproduction (C-1 in (2)) is reduced. Senescence parameters, and male survival rates are held constant during a given run of the model.

In an age structured population with a stable age distribution and a constant rate of growth the relationship between the survival and reproductive rates, and the growth rate of the population is described by Lotka's (1907) equation:

$$l_x m_x e^{-rx} = 1 \qquad (4)$$

where x is age, l_x is female survivorship to age x, m_x is the number of female offspring recruited to the population from each female of age x, and r is the rate of growth. Formulated in this manner, Lotka's equation holds strictly only for birth-pulsed populations (where all the reproduction takes place during a short discrete time period) at a stable age distribution. California sea otters reproduce throughout the year, and so are not birth-pulsed; the stochastic nature of the model precludes attainment of a stable age distribution, even at equilibrium population size, except by fortuitous coincidence. But we assume in the model structure and for purposes of parameter estimation that Lotka's equation provides an adequate approximation to the structure and dynamics of the California sea otter population.

At the beginning of each time step in the model r is calculated according to (3), and then Lotka's equation is solved numerically by adjusting the female early hazards curve until the appropriate l_x schedule is found. Because of the violations in the assumptions of Lotka's equation the stochastic fluctuation in age structure, the survivorship schedule determined at the beginning of each time step will result in a population growth rate that only approximates the rate calculated in (3).

Parameter estimates

Our approach in estimating population parameters was to begin with independently derived estimates, then vary them systematically to arrive at a set of parameters that: 1) were consistent with each other within the structural framework of the model, and 2) were in reasonable agreement with the original empirically derived estimates.

Survival. We estimated annual survival rates from our telemetry data (see Chapter 2) using the method of Heisey and Fuller (1985). The ages at which these rates applied were estimated by calculating an average age for known aged telemetered animals weighted by the number of days each animal was observed:

$$x = x_i d_i / d_i \quad ;i=1,N \tag{5}$$

where x is the age at which the calculated annual survival rate applies, x_i is the age of animal i as determined from tooth annuli (see Chapter 6), and d_i is the number of days animal i was observed. The values in Table 10.1 show the effect on the estimates of using different age thresholds for distinguishing between juveniles and adults. We thus obtained pairs of age-specific annual survival rates for each sex that could be fitted to survival rates calculated from (1).

Table 10.1. Estimates of annual survival rates of telemetered sea otters in California, as determined by the method of Heisey and Fuller (1985), 1983-1986.

	Juveniles		Adults	
Age of adulthood	Average age[1]	Estimated survival	Average age[1]	Estimated survival
FEMALES:				
1	0.61	0.69	5.94	0.91
2	1.41	0.78	7.06	0.92
3	1.88	0.83	7.88	0.92
4	2.16	0.83	8.09	0.91
MALES:				
1	0.38	1.00	4.78	0.73
2	1.26	1.00	6.21	0.68
3	1.92	0.87	6.92	0.71
4	1.94	0.76	6.94	0.77

Separate estimates of annual survival can be obtained from the sample of otter teeth collected from museums and aged

[1] Weighted according to eq. (9) in text.

by counting annuli. The method of age determination and the problems associated with it are discussed in Chapter 6 the distributions of estimated ages are shown in Fig. 10.5. The number of animals represented in Fig. 10.5 is smaller than the total sample because many of the collected animals could not reliably be assigned a sex. The fact that, in the female data, the numbers of animals in the even age classes is consistently higher than those in the odd age classes (except for age 5) is unexplained. And the fact that there are apparently fewer animals of both sexes dying at age one than at age two is questionable, and may be a result of small carcasses not having the same chance of recovery as larger ones (due, perhaps to more rapid decomposition or lower visibility) or that incomplete dentition in some one year olds may have resulted in selection against them when the teeth to be aged were extracted from the museum collections.

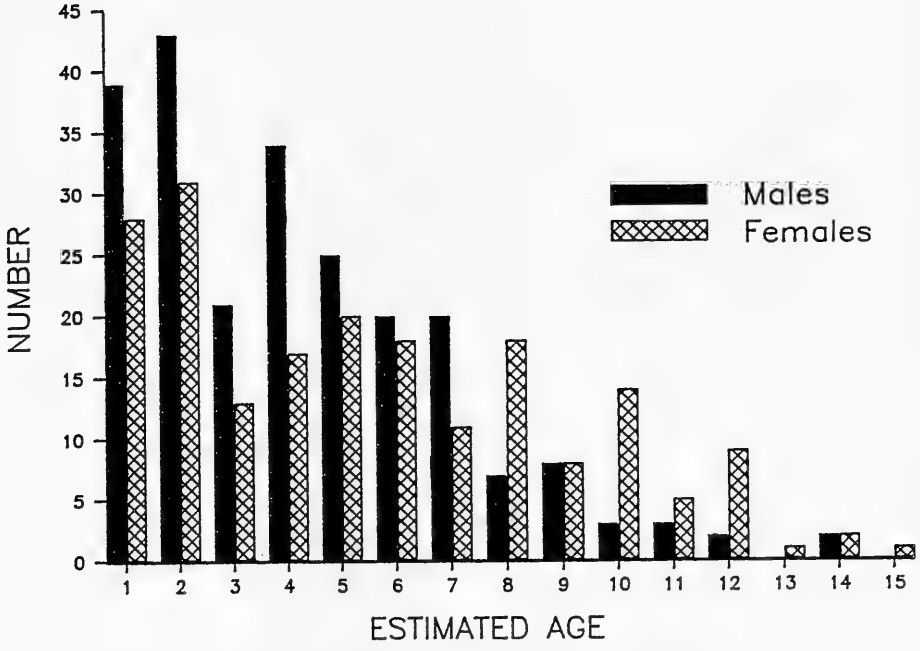
Despite the uncertainties in the tooth data, we did calculate annual survival rates using the "segment" method (Chapman and Robson 1960), which assumes constant annual survival after a threshold age, to compare to the estimates obtained from the telemetry data. Assuming a stationary population:

$$d_x = N(l_x - l_{x+1}) = N(l_c s^{x-c} - l_c s^{x+1-c}) = Hs^x \quad (6)$$

where N is the total population size, d_x is the number of animals dying at age x, l_x is survivorship to age x, s is the constant annual survival rate, c is the threshold age, and H is the constant represented by: $dl_c(1-s)s^{-c}s^x$. Using the Chapman and Robson (1960) regression to estimate a constant annual survival rate between ages four and ten (i.e. c =4 in (6), data for teeth older than 10 were not used) yielded a female rate of 0.925 (s.e. =0.045) and a male rate of 0.723 (s.e. =0.038). If we assume that actual survivorship is as in (1), the ages from four to ten represent the segment that has survived the early hazards but is not yet greatly affected by senescence. If we further assume that the Chapman-Robson method estimates average survival during that age segment, we can calculate the age at which the estimate applies (as we did for the telemetry data) by calculating weighted average ages of the samples in the segment. The weighted averages imply that the female rate applies at age 7.63 and the male rate applies at age 6.40.

The tooth data can also be used to estimate a_1, the early hazard coefficient in (1). Ignoring the portion of the sample greater than 10 years old allows us to ignore the senescence

FIGURE 10.5 -- Distribution of ages of 425 California sea otters estimated by tooth cementum annuli technique.



terms in (1), and, assuming that the early hazards are over by age two, the proportion of animals dying at ages one or two is:

$$p = (1-s_F s^2)/(1-s_F s^{10}) \quad (7)$$

where s_F is the survival rate against early hazards (i,e., $-\ln(a_1)$) and s is the adult survival rate. Using the adult rates calculated above yields a female early risk coefficient of 0.051 (s_F =0.95). The calculation for males yielded an illogical value of 0.270 (s_F=1.31), indicating that the number of 1 year olds may indeed be underrepresented in the sample, and making the female early survival estimate suspect also.

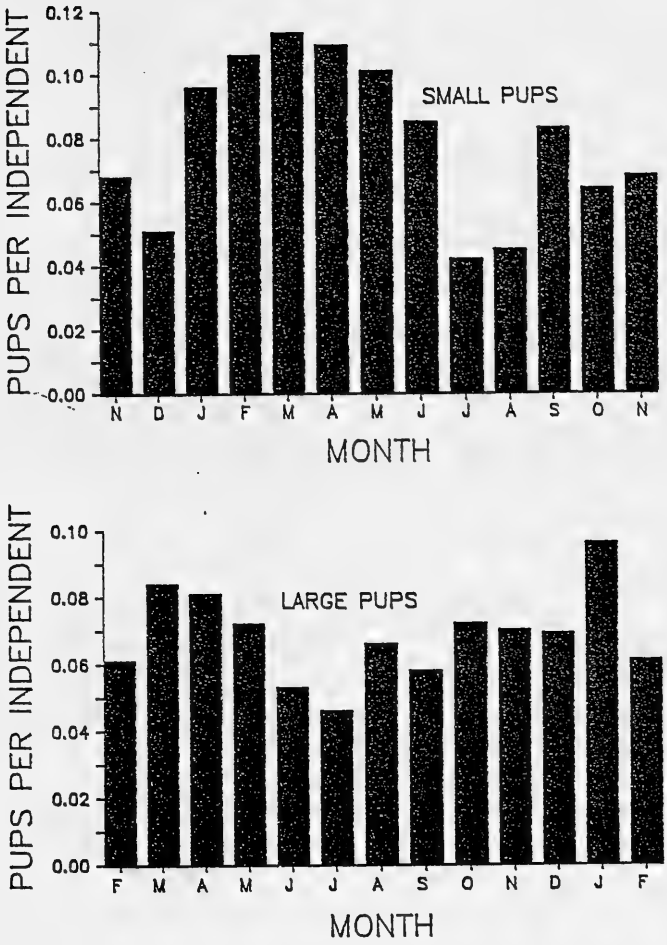
Reproduction.--Since m_x and A in (2) are in terms of offspring weaned, they in turn are functions of pregnancy rates
and pup survival rates. Otters give birth to a single pup, twinning is rare enough to be neglected in calculations. Loughlin et al (1981) suggest a gestation period of four to six months, a pup dependency period of four to eight months, and annual reproduction. Wendell et al (1984) report annual reproduction and a pup dependency period of five to eight months. The longest period that we observed a radioed female associating with a pup was about six months. We use constant gestation and pup dependency periods of six months each in our model. The pupping interval observed in our telemetered animals was not significantly different from one year (see Chapter 2).

Our telemetry data yielded a pup survival (from birth to 6 months) estimate of about 0.50 (see Chapter 2). Assuming no interuterine mortality, a gestation period of six months, and a pup dependency period of six months, this rate translates directly to an annual survival rate of fetuses.

A separate estimate of the ratio of pup survival to adult survival was derived from unpublished CDFG data collected in index areas at monthly intervals between 1976 and 1982 (Wendell et al 1986). These data were counts of independent otters and pups, and the pups were divided by size into a small stage (here assumed to be from 0-3 months old) and a large stage (here assumed to be from 3-6 months old) (Fig. 10.6). Average relative pup survival rate was estimated by contrasting relative numbers of large pups with the peak number of small pups three months earlier. If s_1 is the average survival of independent otters in a given three month period, and s_0 is the survival from the small pup stage to the large pup stage, relative numbers of independents (I), large pups (L), and small pups (S) can be expressed as:

$$L/I = (S/I)(s_0/s_1) \quad (8)$$

FIGURE 10.6 -- Relative average number of small pups and large pups, by month, in the CDFG index areas, 1977-1984.



and, if q is average pup survival relative to adult survival,

$$q = s_0/s_1 = (L/I)/(S/I) \quad (9)$$

From the CDFG data q = 0.439/0.607 = 0.723. The observations were taken three months apart; if we assume that q measures survival over a three month interval, the relative monthly survival is the cube root of q, =0.898. This relative rate can be used to calculate an absolute estimate of pup survival once the adult survivorship schedule is determined.

Using the pup survival estimate derived from telemetry, and assuming a 99% pregnancy rate for prime aged animals and an even sex ratio at birth, the prime weaning rate (A in (2)) is 0.50*0.99*0.5 = 0.247. In the model pup survival is held constant over all maternal age classes, and age specific weaning rates are achieved by varying pregnancy rate with age.

The age of first reproduction for female sea otters in Alaska appears to be about four years (Schneider 1972), although limited observation in California suggests that some otters may reproduce as early as three years. If age at first reproduction is taken as 4 the parameter C in (2) is set at 3.

Senescence.--In sea otters, which are not subject to heavy natural predation or killing (gillnet, shooting or harvest) by humans, and which exhibit low reproductive rates and long lifespans, the senescence parameters are likely to be more important than for many other mammalian species. Siler (1979) relates a_3 and b_3 from (2) and (5) to the modal age of senescence and the standard deviation around that age:

$$a_3 = \exp(-T/S) \quad (10)$$

and

$$b_3 = 1/S \quad (11)$$

where T is the modal age of senescence and S is the standard deviation. The senescence parameters can thus be derived from estimates of T and S. Data from Schneider (1978) suggests that the modal age of senescence in Alaska otters may be 16 years. Eberhardt (1985) found a significant correlation between T and S for 10 species of large mammals. A regression of the data presented by Eberhardt (1985) yielded:

$$S = 0.161 + 0.144T \quad ;(R^2=0.84) \quad (12)$$

Using this equation and a modal age of senescence of 16, the standard deviation of age of senescence is 2.46, a_3 = 0.0025 and b_3 = 0.41.

Density-dependence.--Analysis of historical range expansion and population size data for the OTRANGE model, discussed elsewhere in this report, suggested values of 0.09, and 0.035, for r_{max} and b, respectively, in (3). Given the present length of the range and USFWS (1986) estimates of substrate-specific carrying capacities, the model uses a default value of 1920 animals for K.

Reconciliation of estimates.--A "spread-sheet" type program was set up to allow testing of adjustments in the parameter estimates. Equations (1) and (2) contain a large number of parameters relative to the number of "data points" available to use in estimating them; unstructured numerical solutions to (1) based on annual survival rates at only two ages undoubtedly would be degenerate. The "shape" parameters (b_1, b_3, b_A in (1) and (2)) are particularly difficult because of their abstractness and their potentially large effect on the survival and/or reproductive rates at certain ages. We thus structured our search for the best parameter estimates as follows:

Siler (1979) describes the time constant at which maturity is approached (i.e., the rate at which the early risk becomes asymptotic) as $1/b_1$. In five mammal populations $1/b_1$ was always less than one, with the value of b_1 ranging from 1.06 to 3.84. We conservatively set b_1 equal to one for both males and females, giving a relatively slow approach to maturity, and emphasizing the apparently intense interspecific competition and reduced survival that young female sea otters experience. Similarly, b_A, which governs the rate at which the prime reproductive rate is approached, was set equal to one. The relationship between the senescence parameters, b_3 and a_3, was held initially at the relationship suggested by Eberhardt (1985), and (12) above, and modal age of senescence was varied to affect the shape of the survivorship and reproductive curves through the adult ages. The prime reproductive rate was set at 0.25 and held constant to start with, and a_1, a_2, and the modal age of senescence were varied to find estimates combinations of survivorship and reproductive schedules that: 1) were in reasonable agreement with estimated annual survival rates, 2) produced sex ratios of independent animals in the simulated population in reasonable agreement with those seen in the wild (i.e., female-biased), and, 3) provided reasonable survivorship schedules at all population growth rates between r_{max} and $-r_{max}$. Annual survival rates were calculated from constructed survivorship schedules by :

$$s_x = l_x / l_{x-1} \qquad (13)$$

where s_x is annual survival rate at age x and l_x is survivorship to age x.

Following this approach, we arrived at the parameters given in Table 10.2; these are the default model parameters. With these parameters exp(-a1) (early survival rate) in (1)

Table 10.2. Default parameters used in OTPOP and LESLIE.

Parameter	Equation in text	Value
Maximum per capita growth rate	r_{max} in (3)	0.085
Non-linearity of density dependence	b in (3)	0.020
Equilibrium population size	K in (3)	1720
Adult female risk coefficient	a_2 in (1)	-ln(0.93)
Female modal age of senescence	T in (10)	15
Standard deviation of female age of senescence	S in (11)	2.46
Female senescence risk coefficient	a_3 in (1)	-ln(0.9977)
"Shape" parameter for female early hazards risk	b_1 in (1) and (2)	1
"Shape" parameter for female senescence risk	b_3 in (1) and (2)	0.41
Prime reproductive rate	A in (2)	0.25
"Shape" parameter for approach to prime reproduction	b_A in (2)	1
Age before first reproduction	C in (2)	3
Adult male risk coefficient	a_2 in (1)	ln(0.87)
Male modal age of senescence	T in (10)	9
Standard deviation of male age of senescence	S in (11)	3.5
Male senescence risk coefficient	a_3 in (1)	-ln(0.9264)
Male early hazards risk coefficient	a_1 in (1)	0
"Shape" parameter for male senescence risk	b_3 in (1) and (2)	1

for females varies from 0.96 when the population growth rate is 0.09 to 0.41 when the population growth rate is $-r_{max}$; $\exp(-a_2)$ (incidental survival rate) for females is 0.93, dropping to 0.91 when $r = -r_{max}$, and increasing to 0.97 when $r = r_{max}$ (Fig. 10.7). The age of first reproduction is lowered to three years when $r > 0.06$ (Fig. 10.8). The modal age of senescence for females remains constant at 15 years. The fit of the various estimates of female survival rates to the default model rates for r=0 is shown in Fig. 10.9.

For males, the early hazards survival rate is set at one ($a_1 = 0$, if a male survives weaning there are no additional hazards associated with youth, the value of b_1 for males is thus inconsequential), but the incidental survival rate ($\exp(-a_2)$) is 0.87, and the modal age of senescence is nine years. A modal age of senescence of nine years implies, by (12), a standard deviation of 1.46 years around that age, values of a_3 and b_3 calculated as such and combined with the previously determined rates for a_1 and $_a2$ gave a good fit to the two survival estimates, but led to there being no males over 12 years of age in the population. This is obviously unrealistic, as four of the 219 male teeth were estimated to be 12 years or older. Adjusting the standard deviation of senescence upwards to 3.5 years led to a good fit of the annual survival estimates and ensured that male otters could survive until 16 years of age. The low modal age of senescence combined with a relatively large standard deviation results in the effects of senescence being manifest in the male survivorship curve at an early age (Fig. 10.10). This may seem anomalous, but if the concept of "risk of senescence" in males is stretched to include the risks associated with holding a breeding territory against younger animals, and if these risks include a mortality rate that increases with the years that an animal is not able to hold a territory, the curve may be biologically justified.

With a population per capita growth rate (r) of zero, the predicted sex ratio in the independent population under this parameterization is 0.755 males per female (Fig. 10.11). When r =0.9 the predicted sex ratio is .572 males per female; when r=-0.09 the predicted sex ratio is 1.06 males per female.

Using the survivorship schedules described above with r=0, the average annual survival rate of independent otters is calculated as:

$$S' = \sum_{x=0.844} (l_{xy} / l_{xy}) * s_x \qquad (14)$$

taking the 12th root yields an average monthly survival rate of 0.986. Using the relative pup survival rate calculated

FIGURE 10.7 -- Age-specific female survivorship curves and annual survival rates at different per capita growth rates, under the default population parameters used in OTPOP and LESLIE.

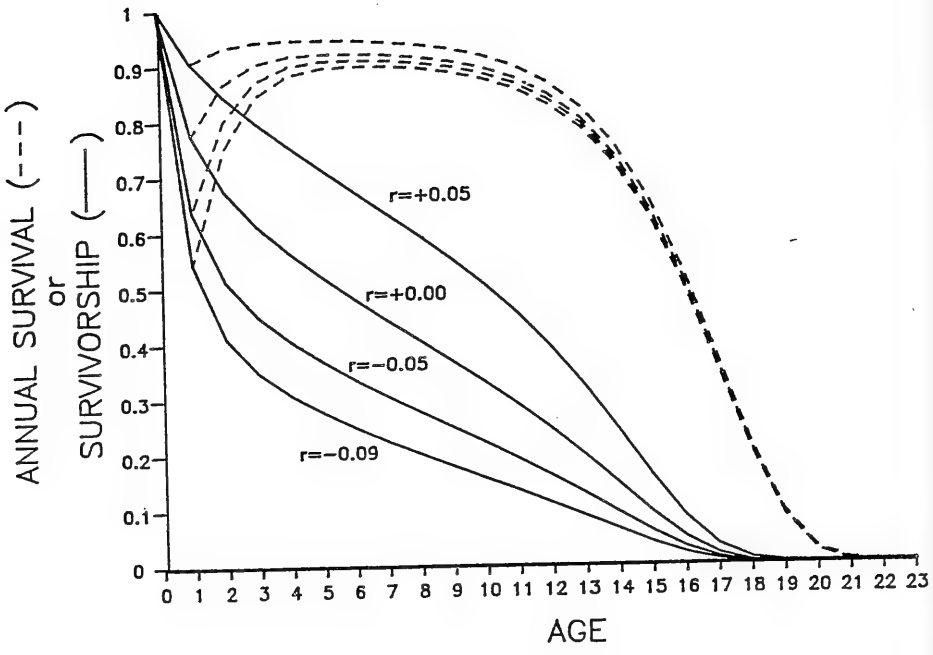


FIGURE 10.8 -- Age-specific reproductive rates under the default population parameters used in OTPOP and LESLIE.

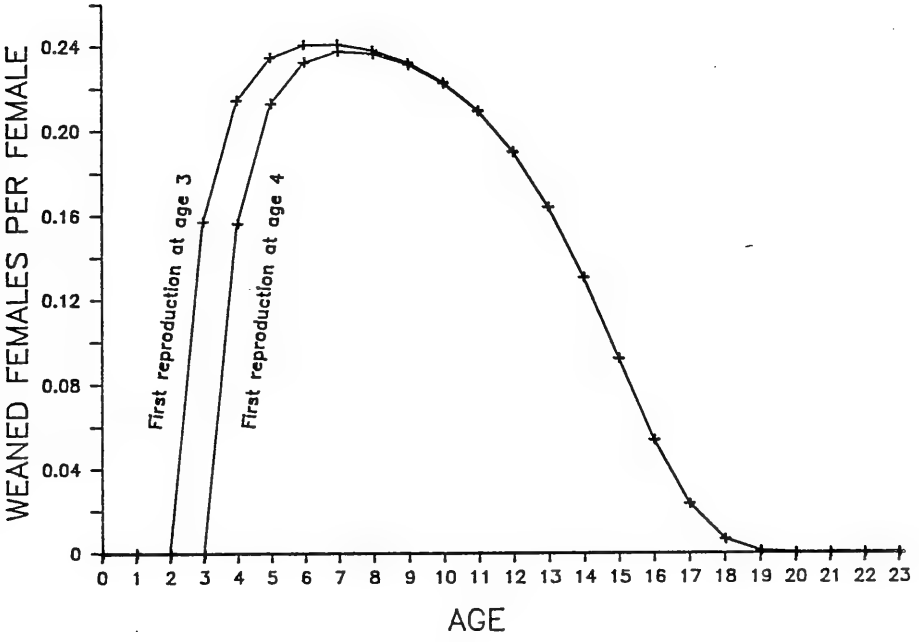


FIGURE 10.9 -- Age-specific female California sea otter annual survival rates calculated under default model parameters and a per capita growth rate=0 compared to survival rates estimated from field data. See text for explanation of estimates.

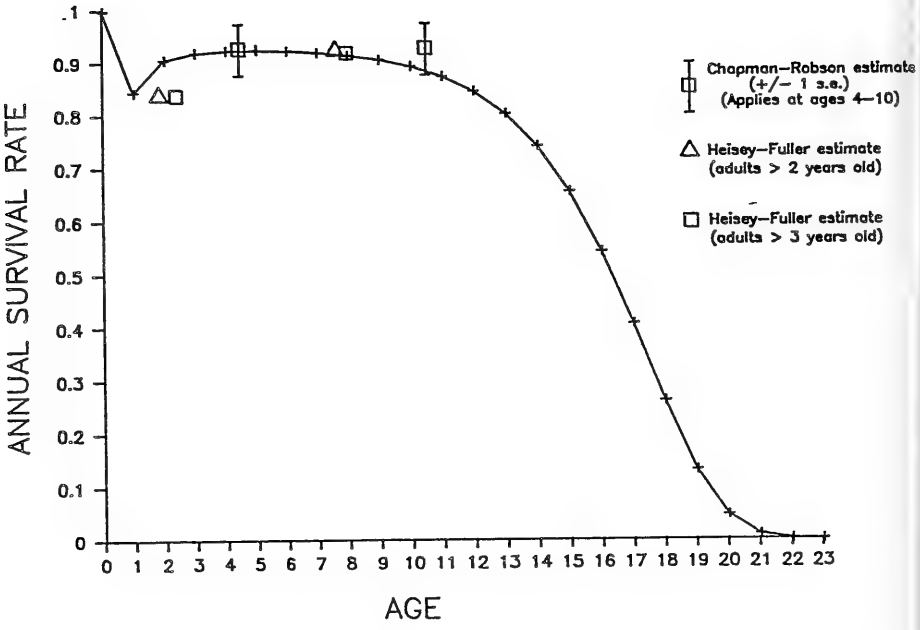


FIGURE 10.10 -- Age-specific male California sea otter annual survival rates calculated under default model parameters and a per capita growth rate=0 compared to survival rates estimated from field data. See text for explanation of estimates.

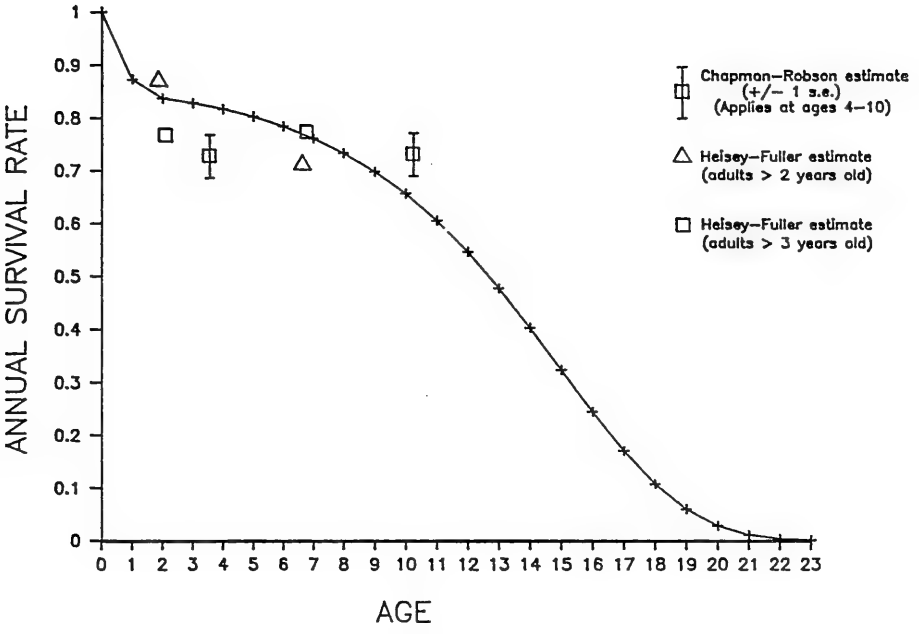
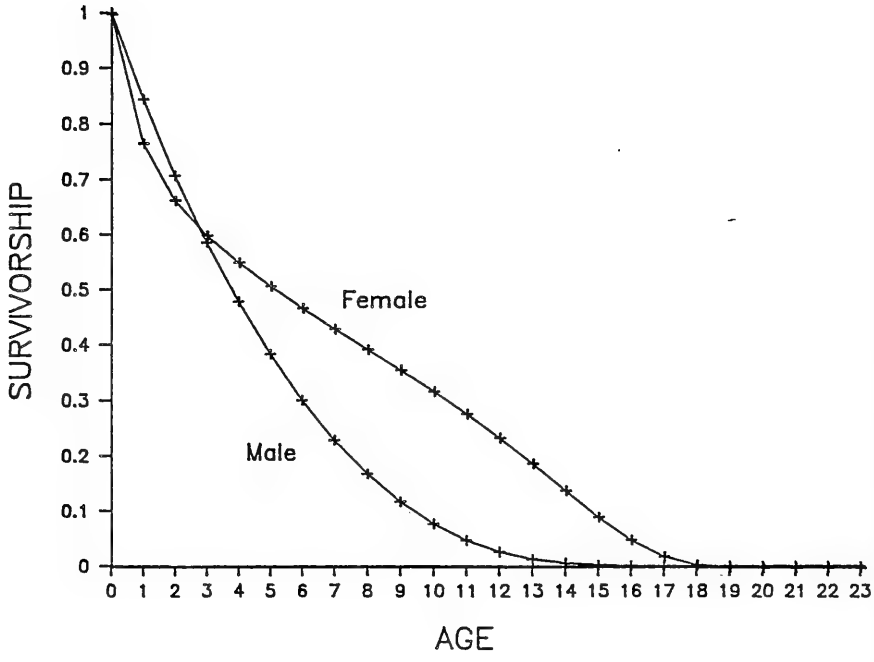


FIGURE 10.11 -- Male and female California sea otter survivorship curves under the default population parameters used in OTPOP and LESLIE and a per capita growth rate=0.



above in (9), the absolute monthly pup survival rate is then 0.986*0.898=0.885, and an annual rate (assuming six months dependency, six months gestation, and no interuterine mortality) of 0.482. This is not too distant from the 0.50 derived from the telemetry data when it is realized that the index areas, being areas of relatively high pup abundance, certainly contain a higher proportion of females than in the population as a whole, and the average adult survival rate as calculated above thus underestimates the average survival of adults in the index areas. By contrast, the average annual female survival rate (calculated as in (14) but ignoring males), is 0.87, and the annual pup survival rate calculated with that rate is 0.499.

It should be reemphasized at this point that the parameter estimates supplied above are the model default values. They may be easily changed by the user to examine the effects of alternative parameterizations, or if future research allows refinement of the estimates.

Seasonality.--The CDFG index area counts indicate a pronounced seasonality in the abundance of pups; this additional complexity in sea otter reproduction is taken into account in the model. The abundance of small pups in the index areas (Fig. 10.6) and the pooling across years (Fig. 2.1, Chapter 2) indicated a peak of pup production in March and a low point in June or July; the biological basis for this seasonality is as yet unknown, it may be due to favorable pup-rearing conditions in the spring and summer leading directly to a synchronous breeding season, or it may be that pups born in the fall suffer high mortality and the females rebreed immediately. We model the seasonality descriptively, assuming a constant monthly pup mortality, and a constant monthly base rate of pupping, adding a seasonal pupping rate to give the observed spring peak.

With a basic year round rate yielding 0.05 pups per independent as a starting point, and assuming that the small pup stage lasts three months the basic monthly rate is 0.05/3.0 = 0.0167. An increased seasonal rate for December to April was then fit to the data in Fig. 10.6 by a numerical least squares procedure. This added increment was 0.02, making the monthly pupping rate for the December through April 0.0167+0.020 = 0.0367. Since these rates were based on relative numbers of pups and independents the ratio of peak monthly pup production to basic monthly pup production, 0.0367/0.0167 = 2.21 is the important parameter. The model uses this ratio and the age-specific pregnancy rates to determine the probability of conception in each month. The annual pregnancy rate is decomposed into the two relative pupping rates by numerically solving:

$$(1-p) = (1-u_1)^7(1-u_2)^5 \qquad (15)$$

(i.e., the probability of not conceiving during the year is the product of the monthly probabilities of not conceiving) where p is the age-specific annual pregnancy rate, u_1, is the basic monthly pupping rate, u_2 is the peak monthly pupping rate, and $u_2 = 2.21u_1$. Intrauterine mortality is again assumed to be zero, and gestation is again assumed to be six months, so that the conception rate for November through May is u_1 and the conception rate for June through October is u_2.

Age specific pregnancy rates for use in OTPOP are calculated according to:

$$p_x = 2m_x \,/\, \{1-(1-s_x)-(1-s_0)+(1-s_x)(1-s_0)\} \qquad (16)$$

where p_x is the annual pregnancy rate for females of age x, m_x is the reproductive rate from (2), s_x is the annual survival rate for females of age x (as in (13)), and s_0 is the annual pup survival rate. This calculation assumes an even sex ratio at birth and assumes that the number of animals weaned in a year ($2m_x$) will be the number of pregnancies minus the number of females that die during the year ($1-s_x$) minus the number of pups that die during the year ($1-s_0$). Because pup death is not independent of maternal death (if a mother dies her pup dies also) the interaction term, $(1-s_x)(1-s_0)$, is added. The age specific pregnancy rates are used to calculate age specific monthly conception rates according to (15). The pattern of monthly pup production generated by OTPOP appears in Fig. 10.12.

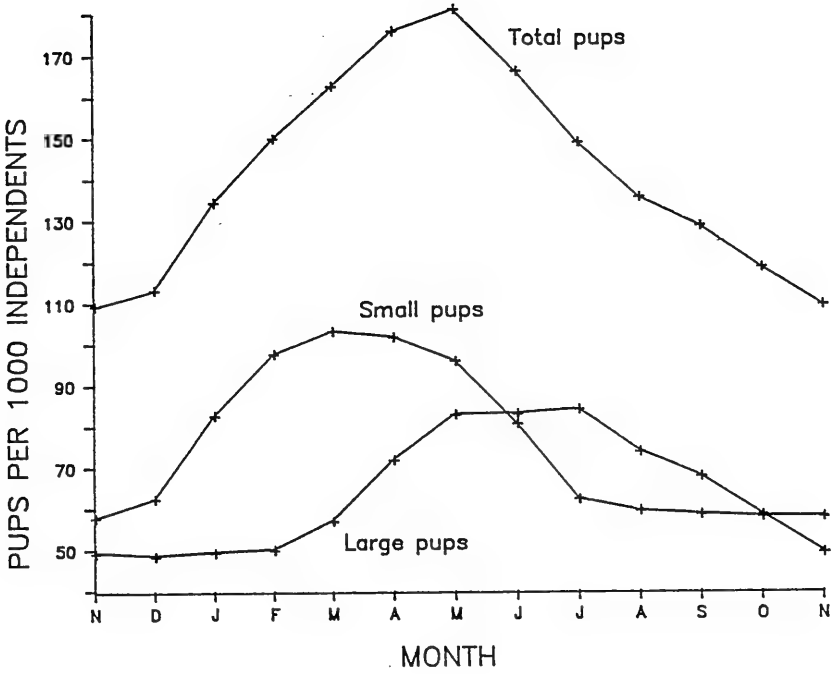
In LESLIE maternal deaths are not considered in the calculation of pregnancy rates because in the life table formulation using an annual time step only the animals that survive the year are available to reproduce, so pregnancy rates are:

$$p_x = 2m_x/s_0 \qquad (17)$$

Constructing an initial population

The population growth rate for the first year of simulation is determined according to the density dependence function (3) given the initial population size and the carrying capacity supplied by the user. Survivorship schedules for each sex are calculated according to (1) using the population growth rate and the sex-specific risk parameters and senescence functions. The proportion of the

FIGURE 10.12 -- Pattern of monthly pup abundance produced by OTPOP. Crosses represent the mean of 85 years of simulation.



population of each sex in each year class is then determined by:

$$V_{xy} = e^{-rx}l_{xy} / \quad e^{-rx}l_{xy} \quad ;x=1,W,\ y=1,2 \qquad (18)$$

where V_{xy} is the proportion of the population of age x and sex y.

Initial conditions require a distribution of ages in months within each age class, and an initial distribution of female reproductive state. Deterministic simulations convinced us that, given the relative conception rates described above, the distribution of reproductive status (and thus of month of birth) converges to a stable distribution from any initial distribution within a small number of iterations. This stable distribution depends on both the basic conception rate (u_1) and the pup survival rate. In any run of OTPOP the pup survival rate is constant, but the conception rate varies by age according to (2) and (16). An average basic conception rate, weighted by the initial stable age distribution, is calculated; beginning with an initial uniform distribution of reproductive states the distribution is simulated deterministically for 15 years on a monthly basis. From the final (assumed stable) distribution of reproductive status a distribution of month of birth is extrapolated, and then these distributions are converted to cumulative density functions.

The age in months of each independent animal in the initial population is determined by a random draw from the month of birth function. The number of pups and fetuses in the initial population is extrapolated from (18) given the initial population size and assuming a stable age distribution. The required number of pups and fetuses are distributed through the female age classes in proportion to the elements of the $l_x m_x e^{-rx}$ vector, and the age of each pup or fetus within each female age class is determined by a random draw from the cumulative density function of reproductive status. Initial conditions generated in this manner alleviate the need for long runs of the model prior to introduction of an oil spill.

OTDIST

Structure

OTDIST distributes the simulated population along the coast. It differs from the other submodels in the fact that it is not dynamic. In OTDIST we assume that the position of an individual otter along the coast is a function of the animal's sex and reproductive status, the month of the year,

empirically derived population density functions, and empirically derived local sex ratios.

We have digitized the coast and the associated five fathom ordinate system for use in the model (Appendix 10.1). For certain aspects of the model it is useful to consider the coast in discrete divisions; in these cases we have used the 40 coastal segments delineated by the CDFG and USFWS in their carcass recovery efforts.

Two density functions are used as input for OTDIST, one giving the density of otters at any point along the coast in May, the second giving the density in December. Similarly, functions giving the sex ratio in each of the 40 coastal segments in May and December are required input for the model. The first step in the distribution procedure is to determine local sex ratios and a density function for the desired month of the year by linear interpolation between the May and December functions. Then the density function and local sex ratios are combined to arrive at density functions for each sex by multiplying the density at each point along the coast by the proportion of each sex at that point.

The female density function is then converted to a cumulative distribution function, and the program loops through the female age vector, determining each animal's position by generating a random number and finding a corresponding location in the cumulative function.

After the females have been distributed OTDIST distributes territorial males. First potential territories are set up along the entire coast. Territory size is assumed to be normally distributed, the location of potential territories are determined by generating lengths from a normal distribution with empirically derived parameters, and stacking them along the coast. Coastal substrates are classified as either rock or sand, as determined from U.S.G.S. topographic maps; only rocky areas are allowed to be potential territories, as no territorial males have been observed in sandy areas in California (B. Hardy, pers. commn).

Once the locations of potential territories are determined, the territorial status of each male in the population is determined. Males six years old and older are potentially territorial. The probability that a potentially territorial male will actually be on a territory is viewed as a function of month of the year, and determined as follows:

$$P(t) = P(a)\ (1-P(d)) \qquad (19)$$

where P(t) is the probability of being on a territory, P(a) if the probability of having arrived on a territory, and P(d)

is the probability of having departed a territory. P(a) and P(d) are assumed normally distributed with empirically derived parameters. The program then loops through the male population vector; when a male of 6 years or greater is encountered a random number is generated and compared to P(t) to determine territorial status. If the male is territorial the location of its territory is determined by generating another random number and finding a corresponding location in the cumulative distribution function for females. The length of coast encompassed by this territory is then made unavailable to non-territorial males by setting the male density function equal to 0 at all points within the territory. If a male draws a territory that is already occupied by a territorial male he is moved to the closest available unoccupied territory.

The last step in the program is to distribute the non-territorial males. The male density function, as modified by territoriality, is converted into a cumulative density function. Another loop through the male population vector is executed; if a male does not have a territory a random number is generated and the corresponding location in the male cumulative distribution function is found.

Once the positions of all animals in the population have been determined, the population and location vectors are passed to OTMOVE, the short term movement and oil response model. The locations of males occupying territories are flagged as they are passed to OTMOVE.

Parameterization of OTDIST

Biologically, the spatial distribution of animals in a population can be viewed as a function of the distribution of resources and social interactions amongst the individuals in the population. Our understanding of the actual mechanisms that produce an observed distribution of animals from the underlying distribution of resources and social system is very incomplete, so we must be content with modeling the distribution in an essentially descriptive manner, incorporating few mechanisms. OTDIST, the distribution model, has been structured to utilize what data is available on the distribution of sea otters within their range in California.

Density functions.--Required inputs for OTDIST include density vectors for winter and summer, representing the number of animals in each 500m segment of the five fathom ordinate system in November and May, respectively. CDFG and USFWS census data were used to construct these vectors. Dates and methods of the censuses for which we had access to the raw data are given in Table 10.3, census methods are described Wendell, et al., (1986).

Interpretation of the census data suffered from the questions of range expansion mentioned at the beginning of the report. For our analysis the locations of animals recorded on field maps during the censuses were translated to five fathom line ordinates and summed by census and 500m segment. Contiguous blocks of 20 500m segments, representing

Table 10.3. CDFG and USFWS censuses used in analysis of California sea otter distribution.

Date		Total Count	Average Group Size	Method
Year	Month			
1968	Aug	311	5.27	Air
1968	Nov	659	4.92	Air
1968	Dec	409	3.56	Air
1969	Jan	986	5.94	Air
1969	Feb	685	3.26	Air
1969	Mar	942	4.34	Air
1969	Apr	654	5.03	Air
1969	May	315	4.32	Air
1969	Jun	1013	5.30	Air
1969	Aug	528	3.74	Air
1969	Sep	404	3.51	Air
1969	Oct	485	3.13	Air
1970	May	902	5.43	Air
1970	Sep	607	4.40	Air
1971	Feb	719	3.95	Air
1971	Apr	901	3.91	Air
1971	Jul	957	4.65	Air
1971	Oct	712	4.07	Air
1972	Jan	1064	3.81	Air
1972	Apr	772	2.81	Air
1973	Dec	936	3.38	Air
1974	Mar	956	2.14	Air
1975	Jun	1040	2.30	Air
1976	Jun	1148	2.12	Air
1979	Jun	808	2.32	Air
1982	Nov	1334	1.77	Ground
1983	Oct	1222	2.06	Ground
1984	Jun	1567	2.32	Ground
1985	May/Jun	1287	2.14	Ground
1985	Oct/Nov	1212	2.20	Ground

10 km of coast each, were grouped together and totaled by census. The percent of the total count of each census in each block was then calculated and used in an analysis of variance. Since sea otter distribution is generally considered to change on a seasonal basis (USFWS 1986) we grouped the census within

each year by season: winter consisting of November through April, summer consisting of May through October (data were too sparse to attempt analysis by month). ANOVA (Table 10.4) showed significant main effects of both year and location, and of season within year. There was also significant interaction between year or season and location. The situation is represented graphically in Figs 10.13 and 10.14.

Table 10.4 -- Analysis of variance in CDFG and USFWS California sea otter census data, 1968-1985. Dependent variable is the proportion of census total along a 10 km section of coast.

Source	d.f	SS	F	p
Year	13	.06065	3.98	0.0001
Season within Year	6	.01985	2.82	0.0100
Location	40	.41554	8.87	0.0001
Year * Location	362	.18867	0.45	0.9900
Season & Location	127	.10161	0.68	0.9900
Error	240	.28108		
Total Model	548	.78632	1.23	0.0300
Model R^2=0.737				

Variation in distribution due to location and season are easily handled by the structure of OTDIST, but, as mentioned previously, OTDIST is time-independent, and annual changes in distribution (aside, of course, from pure stochastic effects) are not explicitly considered. Distribution of sea otters throughout the range in California has undoubtedly changed since the censuses began. We thus decided that the best parameterization of the density functions would be direct incorporation of the most recent census data. A separate analysis showed a highly significant effect of census method on both total count and on average group size. Ground counts appear to enumerate a greater proportion of the population, particularly that part of the population that is solitary on the day(s) of the census. The relative worth of ground counts versus ground-truthed aerial counts for estimating population size has been the subject of some debate, but for present purposes, that of determining relative distribution, it seems as if the method that enumerates the higher proportion of the population will better estimate relative densities. This contributed to our decision to use only the most recent censuses, as coordinated ground counts did not begin until 1982.

Census data from 1984 and 1985 were converted to probability density functions for each census by dividing each segment total by the total number of animals recorded in the

FIGURE 10.13 -- Contour diagram indicating annual changes in sea otter density in California from 1968-1985. Y-axis represents space (5 fathom line ordinate system, increasing, generally from North to South, in 500 meter increments along the five fathom line), x-axis represents time. Diagram was constructed for CDFG and USFWS census data (Table 3). Individual census counts were totaled by 20km section of coast, and the proportion of the total count in each section calculated. These proportions were then averaged by year to get the values used to produce the diagram. Contour interval is 3% of the individual census total. Expansion of the range is evident at the north and south ends of the diagram.

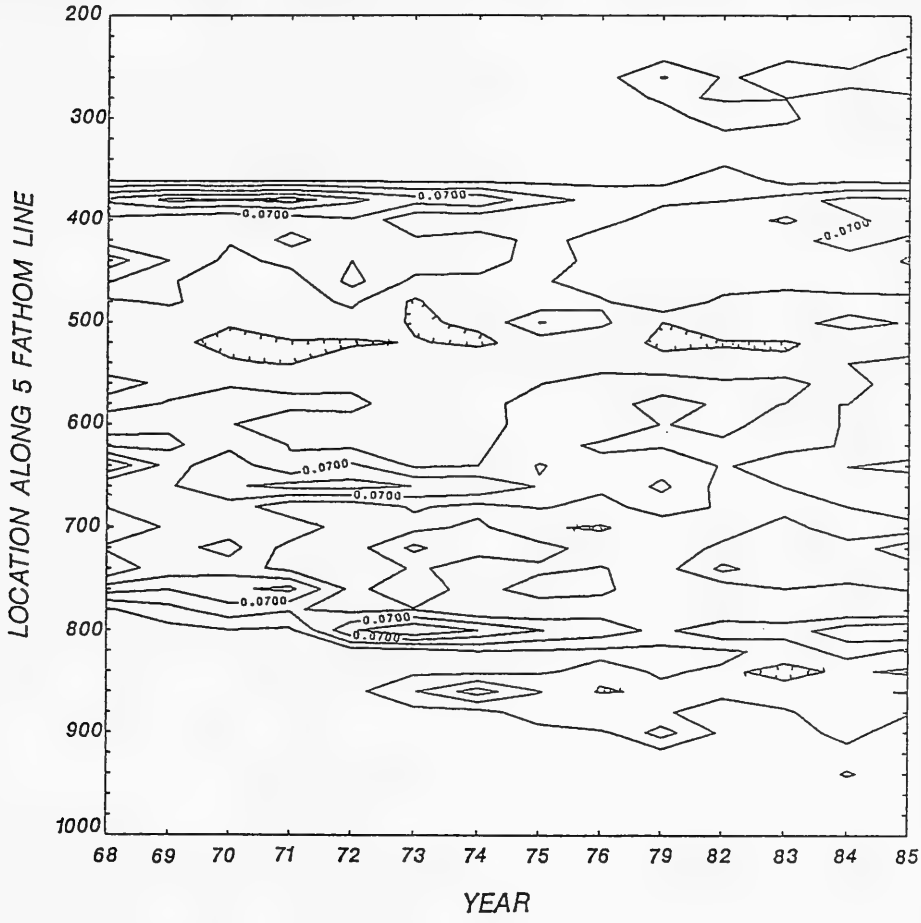
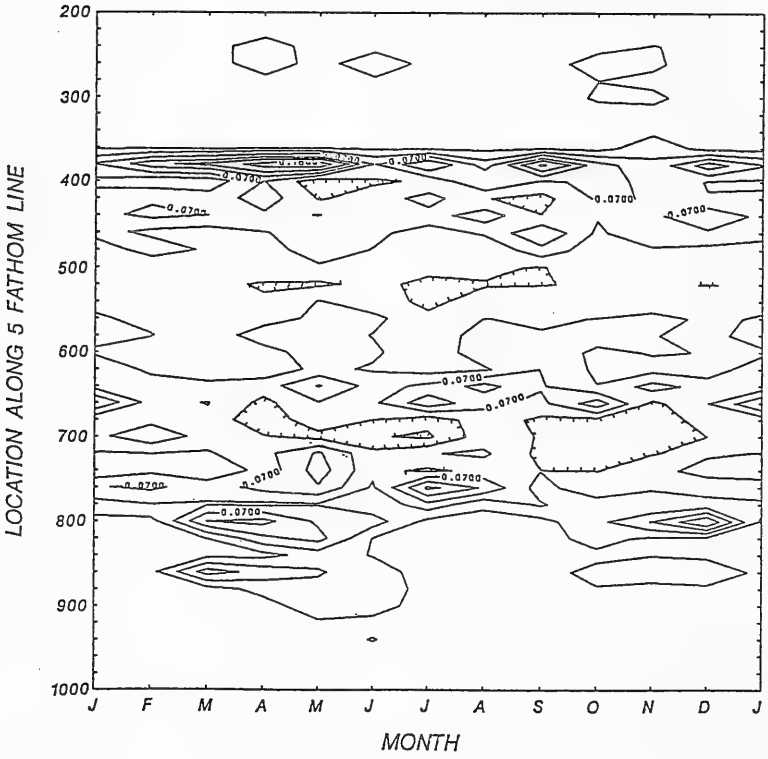


FIGURE 10.14 -- Contour diagram indicating monthly changes in sea otter density in California from 1968-1985. Y-axis represents space (5 fathom line ordinate system, increasing, generally from North to South, in 500 meter increments along the five fathom line), x-axis represents time. Diagram was constructed from CDFG and USFWS census data (Table 3). Individual census counts were totaled by 20km section of coast, and the proportion of the total count in each section calculated. These proportions were then averaged by month to get the values used to produce the diagram. Contour interval is 3% of the individual census total. Seasonal contraction of the range, presumably due to migrations by males, is evident at the north and south ends of the diagram between February and July.



respective census. These density functions were then averaged by season to get the empirical distributions that are used in the model (Fig. 10.15). Approximately 30% of the range is inaccessible by road, and thus is counted by air, even during the "ground" counts. Geibel and Miller (1984), Wendell et al (1986), and Hardy (CDFG, personal communication) report that aerial observers typically enumerate from 50-80% of the animals seen by ground truth observers; the density functions derived from the raw census data are thus further modified by multiplying the densities in portions of the range that are counted from the air are multiplied by 1.3.

It is assumed that differences between the two seasonal distributions are due to seasonal movements of animals, particularly adult males migrating between male areas in the winter and breeding territories in the female areas in the summer. The censuses are timed to reflect the peak of congregation in the male areas and the peak of territoriality, respectively; therefore density functions for each month are obtained by linear interpolation between the summer and winter functions.

The censuses are an integral part of CDFG's and USFWS's sea otter research programs, and are scheduled to continue to be conducted twice yearly in the future. The density functions are stored in an external file so that they can be easily updated after each census and incorporated into the model. USFWS has been supplied with a computer program that allows rapid digitizing of raw census data and outputs the data in an appropriate form for the model.

Sex ratios.--The census data provide distributions for the population as a whole, but provide very little information about the distribution of each sex throughout the range. Some local sex ratio information is available from the carcass recovery data. The location of each recovered carcass is recorded by recovery area (Ames et al 1985). Each recovery area is about 12km long. Sex ratios for each recovery area were calculated, combining all data from December through April and from May through November (Table 10.5).

The carcass recovery data suffers from small sample size in many of the areas, from sampling problems discussed by Ames et al (1984), and, again, from changes in distribution that have occurred as the range expanded. As an alternative we used a delphic technique, asking field biologists from CDFG, USFWS, and other institutions who had been frequent participants in the semi-annual censuses to estimate present seasonal sex ratios in each of the recovery areas. Averaging the responses from the questionnaire gave the sex ratios in Table 10.5 and Fig. 10.16. Each of the respondents was familiar with the carcass recovery data, and most said that

FIGURE 10.15 -- Density functions used in OTDIST for the location of independent sea otters in California in June (dashed line) and December (solid line). Functions derived from CDFG and USFWS censuses conducted in 1985. OTDIST works at a resolution of 50m, but for clarity densities were totaled by 20km sections to construct this diagram. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

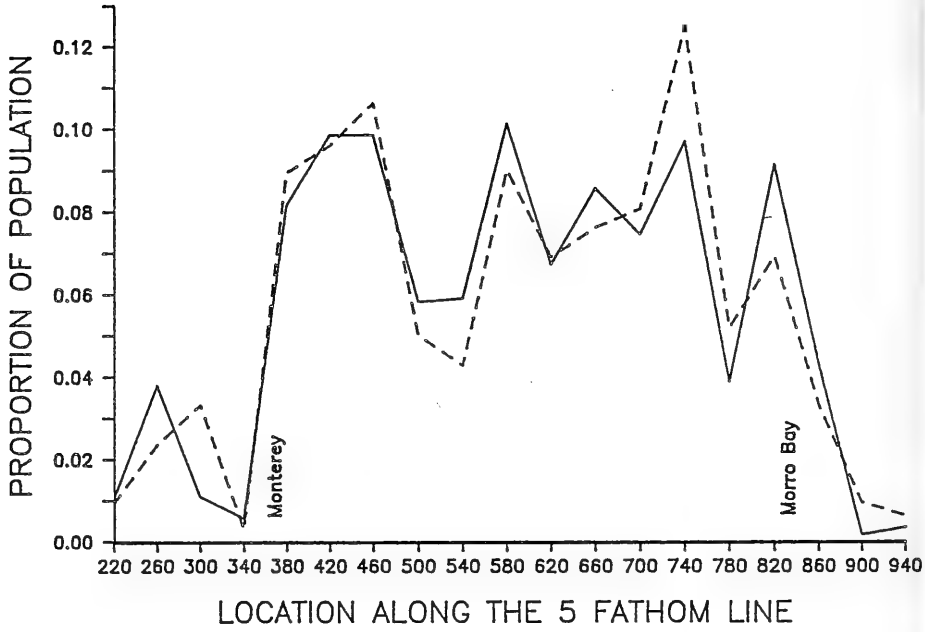
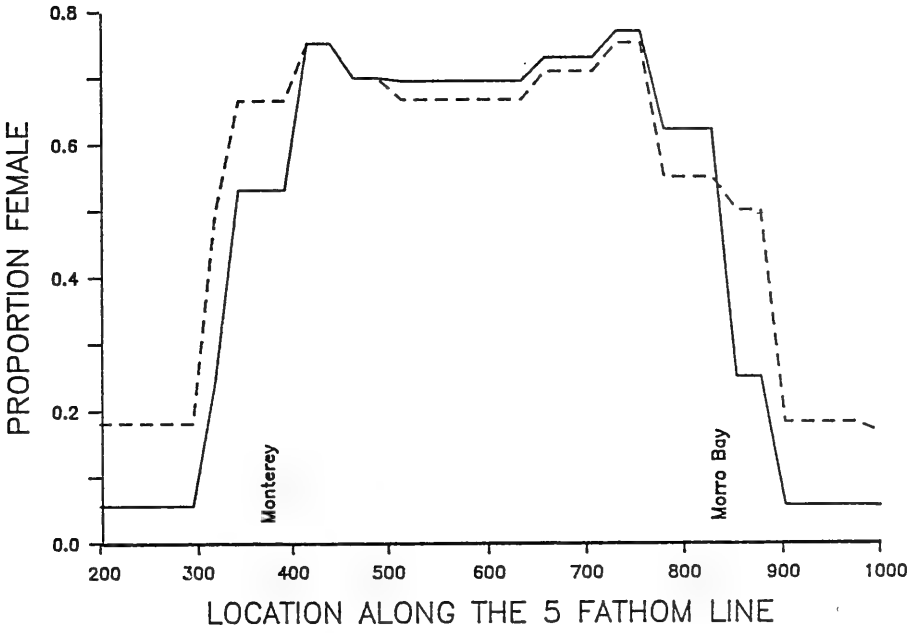


FIGURE 10.16 -- Local proportion of California sea otters that are female in June (dashed line) and December (solid line), used in OTDIST. Data, from questionnaires distributed to knowledgeable biologits, was collected by CDFG carcass recovery area and assumed to apply over the entire section of coast within each recovery area. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.



they used that data as a guideline in making their estimates. We feel that their estimates are more realistic than those that could have been attained by a purely statistical analysis of the sparse data, and therefore used their estimates in the model.

Table 10.5. California sea otter sex ratios of recovered carcasses (1968-1985) and as subjectively estimated by field biologists, by season and CDFG carcass recovery area.

CDFG recovery area[2]	Recovered carcasses May-Oct M	Recovered carcasses May-Oct F	Recovered carcasses Nov-Apr M	Recovered carcasses Nov-Apr F	Subjective estimates May-Oct M/F	Subjective estimates Nov-Apr M/F
<7	3	0	1	0	4.5	16.7
7	1	0	3	3	4.5	16.7
8	1	0	5	0	4.5	16.7
9	1	0	0	3	4.5	16.7
10	2	0	2	1	4.5	16.7
11	42	8	27	6	4.5	16.7
12	26	24	6	1	1.0	3.0
13	36	24	35	30	0.5	0.9
14	20	20	22	13	0.5	0.9
15	2	6	4	5	0.5	0.9
16	16	11	13	23	0.3	0.3
17	2	5	9	16	0.3	0.3
18	11	30	25	48	0.4	0.4
19	3	17	14	16	0.4	0.4
20	1	7	7	13	0.5	0.4
21	1	5	1	1	0.5	0.4
22	2	4	2	4	0.5	0.4
23	0	0	2	5	0.5	0.4
24	0	1	1	0	0.5	0.4
25	0	1	5	1	0.5	0.4
26	0	1	0	0	0.4	0.3
27	3	10	5	6	0.4	0.3
28	16	10	15	17	0.4	0.3
29	18	31	12	30	0.3	0.3
30	10	6	8	2	0.3	0.3
31	16	9	5	7	0.8	0.6
32	70	36	27	18	0.8	0.6
33	25	16	25	12	0.8	0.6
34	2	2	2	2	1.0	3.0
35	5	1	2	0	1.0	3.0
36	22	2	5	3	4.5	16.7
37	33	7	12	5	4.5	16.7
38	4	1	2	0	4.5	16.7
39	0	0	1	0	4.5	16.7
40	2	0	1	2	5.0	17.0

[2] See Appendix 1 for location of CDFG carcass recovery areas.

As for the seasonal distributions, the seasonal sex ratios are assumed to be the result of male migrations to and from breeding territories, and sex ratios for the each month are obtained by linear interpolation. Probability density functions for each sex in a given month are then obtained by multiplying the population density function for the appropriate month by the appropriate sex ratio:

$$s_{ijk} = d_{jk}p_{ijk} \quad (20)$$

where s_{ijk} is the density of sex i, in month j in 500m segment k, d_{jk} is the population density in month j in segment k, and p_{ijk} is the proportion of sex i in month j in segment k, and sex ratio in a recovery area is assumed to apply to all 500m segments in that recovery area (Fig. 10.17).

Parameters pertaining to territoriality.--The model divides the coast into potential territories. Territory length is assumed normally distributed, parameters of the distribution were obtained from Jameson (1987), who reported mean male territory length near Piedras Blancas during 1978-1984 at 1.1 km (s.d. =0.43km, N=13), and our telemetry data. Additional parameters required by the model are mean territory arrival and departure dates, and associated standard deviations. Jameson (1987) gives mean arrival date as 22 May (s.d. =33.6 days, N =16) and mean departure date as 21 December (s.d. =38.1 days, N =18). The proportion of males over the age of six that are territorial at any given time is assumed to vary seasonally between 0.25 and 0.75.

The data from Jameson (1987) provides default values for the male territoriality parameters in OTDIST; but our telemetry data suggests that the highly seasonal pattern of male movements observed by Jameson (1987) during 1978-1984 may not be occurring at the present time or throughout the entire range (see Chapter 3). The user can change the values of the territoriality parameters at the beginning of a model run; setting large standard deviations of arrival and departure dates and/or small differences between the minimum and maximum proportions of males that are territorial will reduce the amount of seasonal variation in male territoriality in the model.

Expanded sea otter range

As mentioned previously, the size of the sea otter range and its carrying capacity are fixed for the duration of any run of the model. Since, however, the peripheral areas of the current range are the most susceptible to oil spills, and it is very possible that the range will continue to expand in the

FIGURE 10.17a -- Density functions used in OTDIST for the location of male (dashed line) and female (solid line) sea otters in California in June. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

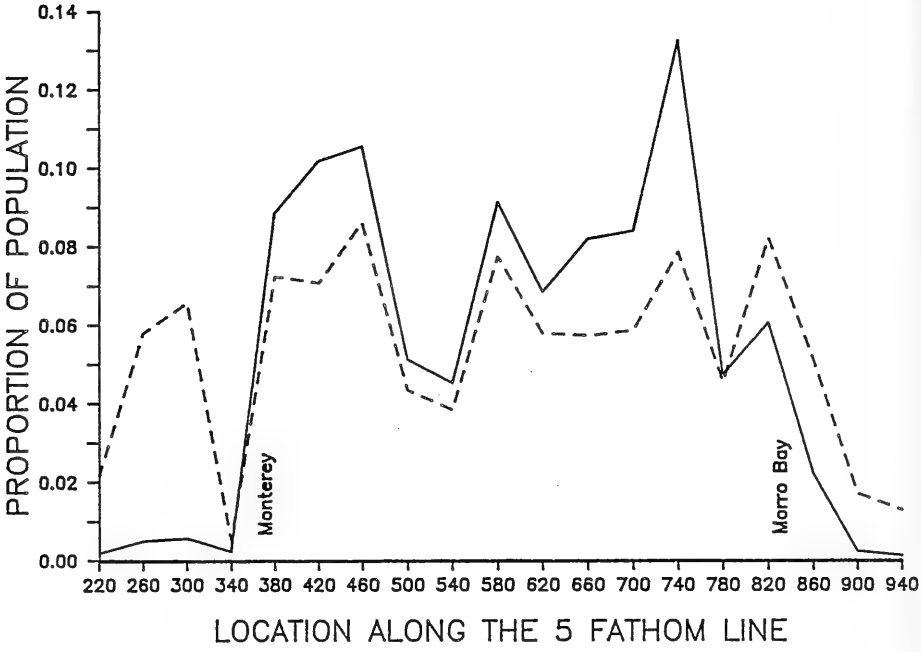
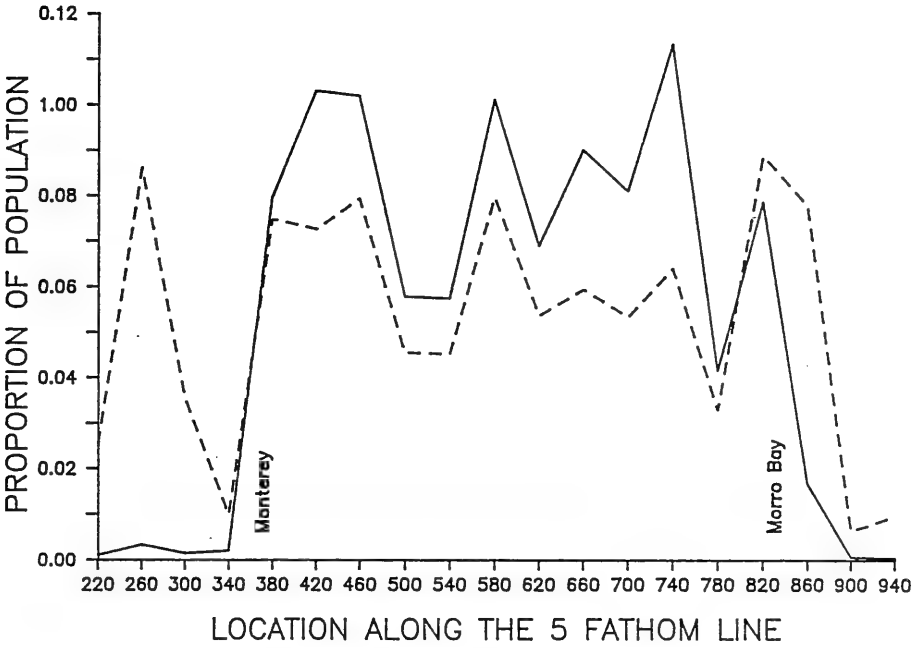


FIGURE 10.17b -- Density functions used in OTDIST for the location of male (dashed line) and female (solid line) sea otters in California in December. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.



near future, we have constructed a simple deterministic model of sea otter range expansion, OTRANGE, which was described earlier. The output from OTRANGE includes projected population sizes, range boundaries, and carrying capacities, which can be used to initialize OTPOP. Obviously, the census data required as input for OTDIST will not be available for the peripheral parts of the simulated range as expanded by OTRANGE. Thus we provide a sub-routine, EXPRAN, that, in the event that the north and south ends of the census data used as input do not coincide with the range boundaries input by the user, will predict the distribution of otters in the expanded range.

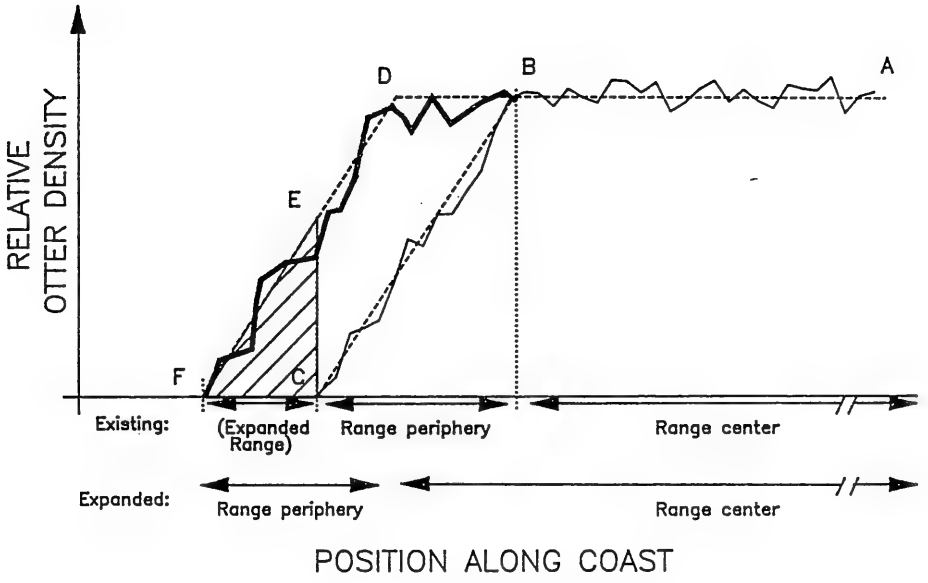
After examination of the data in Figs. 10.13,10.14,10.15, and 10.16, we arbitrarily divided the range into a southern periphery, south of the 840 ordinate on the five fathom line, a northern periphery, north of the 340 ordinate on the five fathom line, and a center, between the 340 and 840 ordinates. Using the density functions constructed by OTDIST from the census data, EXPRAN calculates the average density of otters of each sex in the center of the range (Fig. 10.18, point A), and assuming that the densities at the endpoints of the censused range are zero, calculates the average slope of the distribution through the north and south peripheries (Fig. 10.18, slope S). Density is then extrapolated from the end of the central range into the peripheral range a distance equal to the length of expansion using the central range average density combined with censused deviations from the slope of the peripheral density (Fig. 10.18, line A-B). In this manner the central range is thus considered to have extended into existing peripheral range. Densities in the peripheral part of the range beyond the expanded central part of the range are calculated by adding the difference in density implied by the slope of the peripheral density and the length of expansion (Fig. 10.18, line B-C). Density in the expanded part of the range is made cumulatively equal to the area of CDE in Fig. 10.18, but weighted at any point according to the type of substrate. USFWS (1986) estimates that rocky habitats can support 3.1 times as many otters as sand habitats, this ratio is used in the determining the densities in the expanded range. The heavy line in Fig. 10.18 indicates the new densities calculated by EXPRAN.

OTMOVE

Structure

OTMOVE simulates the movements of the animals in the population on a daily basis for up to 30 days, and checks animal positions against the location of a simulated oil spill. It iterates on a daily time step, and considers

FIGURE 10.18 -- Schematic representation of the algorithm used in EXPRAN to predict sea otter densities in expanded range. See text for explanation.



position at a spatial resolution of 50 meters. The location vectors generated by OTDIST are the initial positions of the animals, the identity of animals dying as a result of contact with the spill are passed to OTPOP.

As in OTDIST, spatial considerations are simplified by conceptualizing the system as one dimensional. Otters are located and move upcoast and downcoast on the five fathom line ordinate system, and oil spills are 1 dimensional also. At the beginning of a run the date, duration (in days), and boundaries of the oil spill are input. Since the purpose of the movement model is to determine the numbers of animals that die as a result of the spill, it runs for only as many days as the duration of the spill. The movements of each animal are assumed independent of the movements (but not the spatial distribution) of the other animals in the population. This allows a structural efficiency of looping days within animals rather than animals within days; the movements of each animal are simulated for the duration of the spill and its fate decided before the next animal is considered.

Each otter in the simulated population is considered to have a home range (or a territory, for territorial males), the center of which is the position assigned to the animal in OTDIST. OTDIST assigns each animal to one of six classes depending on sex and reproductive status: 1) juvenile male, 2) adult, non-territorial male, 3) adult territorial male, 4) juvenile female, 5) adult female without pup, 6) adult female with pup. Juveniles are animals younger than the age of sexual maturity that is used in the population model, males over the age of six years are potentially territorial. Three categories of daily movements are considered in the model: 1) "routine" movements around the home range or territory center, 2) seasonal migrations by territorial males, and 3) movements in response to oil spills. The position of an animal at the end of a simulated day is calculated as:

$$X_t = X_{t-1} + d_t \qquad (21)$$

where t indexes days, X is the position along the five fathom line, and d_t is the daily movement. Negative values of d_t indicate movement up the coast (i.e., toward the origin of the five fathom ordinate system), positive values indicate movement down the coast.

Routine daily movements.--Routine daily movements are modeled as a function of displacement from the home range or territory center, and the magnitude and direction of the previous day's movement:

$$d_t = b_1 d_{t-1} + b_2 (X_t - C) + Z_t \qquad (22)$$

where b_1 is the autoregressive parameter, b_2 is the displacement parameter, C is the location of the home range or territory center, and Z is a normally distributed random error with mean 0. The parameters b_1 and b_2 and the standard deviation of Z vary with class.

Migratory movements.--Migratory movements by adult males are simulated at appropriate times of the year. Territory arrival and departure dates are assumed to be normally distributed, empirically derived means and standard deviations around those dates are used to calculate the probability of a male arriving or departing a territory on each day of the simulation. For territorial males on each day of simulation a random number is compared with the probability of departing a territory in that day For non-territorial but potentially territorial males a random number is compared against the probability of arriving on a territory; to account for travel time to the territory, the mean of the probability distribution is set three days before the actual mean; thus the distribution gives the probability of non-territorial male departing for a territory.

Class two (non-territorial adult) males that are determined to depart their present home range for a territory are assigned destination territories using the cumulative distribution of female positions derived from the female location vector constructed by OTDIST. Since territorial male density is thought to be negatively correlated with pup density (Jameson 1987, USFWS 1987), only the locations of mature females without pups are used to construct the distribution. The destination is compared to the list of potential territories and their statuses (occupied or not occupied) (also generated by OTDIST). If the territory originally assigned as a destination is occupied, the closest (to the original destination) available territory becomes the destination territory. Once a destination territory has been determined, the male moves according to:

$$d_t = i * |V_{max} + Z_t| \qquad (23)$$

where Z_t is as in (22), V_{max} is the maximum daily rate of movement for a class 2 animal and i = +1 if the destination is down the coast from present position and -1 if the destination is up the coast. Once the male has reached the destination territory it moves routinely according to class three parameters.

Class three animals that are determined to leave their territories are assigned destination home ranges by choosing from a cumulative density function constructed from the locations of males generated in OTDIST. Simulated male density in each 500m segment is squared before constructing

the cumulative density function in order to accentuate the aggregation of non-territorial males. Once a destination has been chosen the male moves according to (23) until he reaches the territory, at which point he moves routinely according to (22) with class two parameters.

Movements in response to oil spill.--Each time that a daily movement can bring an otter into contact with the oil spill a series of "decisions" on the part of the otter are simulated, conditional on the spatial relationship between the animal's home range, its present location, and the oil spill. If the animal's home range center is inside the spill boundaries it may elect to abandon its home range and establish a new range outside of the spill with daily probability PE. If the animal's home range center is not within the spill boundaries, or if it is within the spill boundaries but the animal has elected not to abandon the home range, it may attempt to avoid the spill with probability PA. If an animal avoiding a spill with a present location outside of the spill "bounces" off of the spill boundary it moves a distance:

$$B_t = -(d_t - D_t) \qquad (24)$$

where d_t is the predicted daily movement according to (22), B_t is the distance bounced, and D_t is the distance to the oil spill boundary. If an animal elects to attempt to avoid the oil after it is already inside of the spill boundaries it moves according to (23) with the value of V_{max} and the standard deviation of Z appropriate to its class, and the sign of i is randomly assigned with equal probability.

If, at the end of a simulated day, an animal is inside of the spill boundaries (and thus exposed to oil), it dies with probability PM.

Assuming for a moment that PM is very low, a number of behavior patterns in relation to oil on the part of individual animals may occur depending on the values of PE and PA and the size of the spill. Animals might depart the spill area immediately and not return during the life of the spill; animals might spend a few days in the spill and then depart; animals might move routinely outside of the spill; avoiding it by bouncing off when routine movements would ordinarily bring them inside the spill; animals might continue to move routinely on the edge of the spill entering it occasionally; animals might move in a routine manner within the spill; animals might move long distances up and down the coast inside the spill in a "panic".

Parameterization of OTMOVE

Parameters used in the movement model were derived from our telemetry data. The daily locations of radioed animals, recorded in the field on an x,y coordinate system, were moved to the five fathom line ordinate system to simplify the analysis of movement patterns and to derive a parameterization applicable to the single spatial dimension used in the model. Graphic traces of the movements of each animal along the five fathom line are presented in Chapter 3. Two of these are reproduced here for illustrative purposes (Fig. 10.19).

Routine movements.--After original examination of the traces represented by Fig. 10.19 we attempted to analyze the movements of each animal as an autoregressive time series, modeling each day's movement as a function of previous days' movements and/or correlated error terms. This analysis led to good predictive equations for the movements of many of the animals, but the equations for individual animals often differed dramatically in form and degree. With no biological basis on which to decide upon the efficacy of one form of equation over another, incorporation of these equations into the movement model was unjustifiably complicated.

We thus opted for the simple regression equation (22) mentioned previously. One autoregressive parameter is maintained in the equation, but the major factor in the equation is the displacement term. The horizontal lines in the traces of Fig. 10.19 mark the mean position over all days for which data was obtained on each animal. Movements of many animals were characterized by long periods of time above or below the overall mean, but localized oscillations around short term means (Fig. 10.20). Since the movement model is designed to run for at most 30 days, we ignore patterns that occur on a longer time scale, and model the oscillation around short term means. The series of locations for each animal were divided into arbitrary non-overlapping 30 day segments, and regression parameters calculated for each segment (segments wherein an animal was not able to be located for more than 10 of the 30 days were not included, a total of 383 segments were used in the analysis). This parameterization was encouraging, as the displacement terms in all equations were negative, and most were highly significant. We then restratified the analysis, grouping the segments according to the six classes of animals described earlier (30 day segments in which the reproductive status of an adult female changed or was unknown were discarded). The regression parameters and the standard deviation of the errors are given in Table 10.6; these are the default values used in the model.

FIGURE 10.19a -- Daily locations of a juvenile female California sea otter (#35) as determined by telemetry, 1985-1986. Location is given in 50m units south of San Francisco, along the 5 fathom line ordinate system. Horizontal line is the mean position of all daily locations. Julian date 1 is 1 January 1984. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

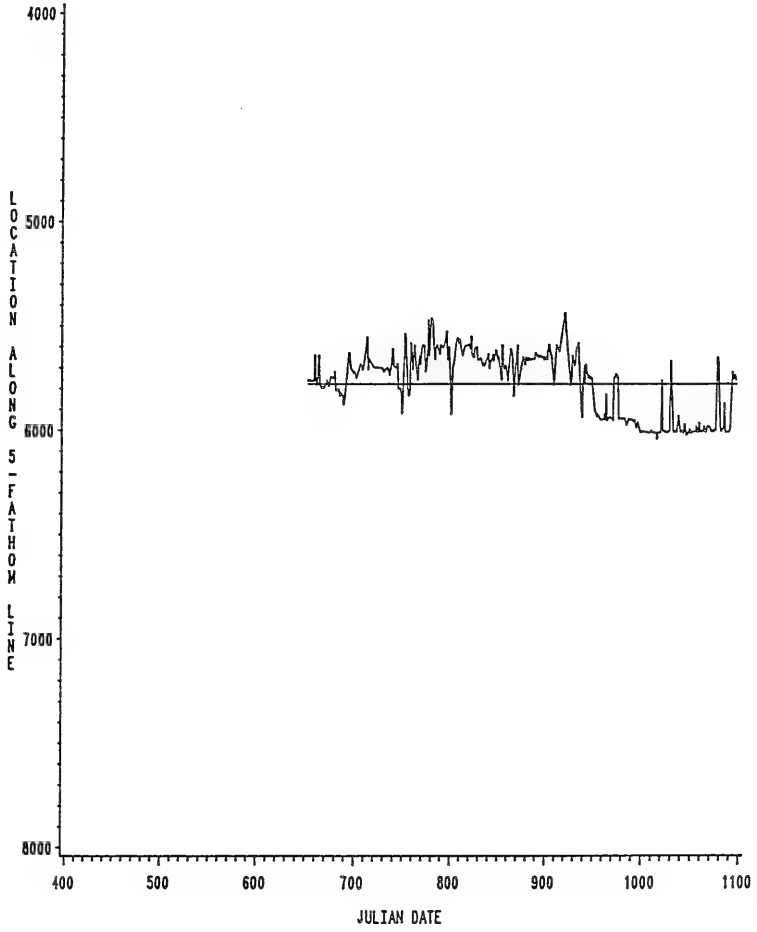


FIGURE 10.19b -- Daily locations of a juvenile female California sea otter (#29) as determined by telemetry, 1985-1986. Location is given in 50m units south of San Francisco, along the 5 fathom line ordinate system. Horizontal line is the mean position of all daily locations. Julian date 1 is 1 January 1984. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

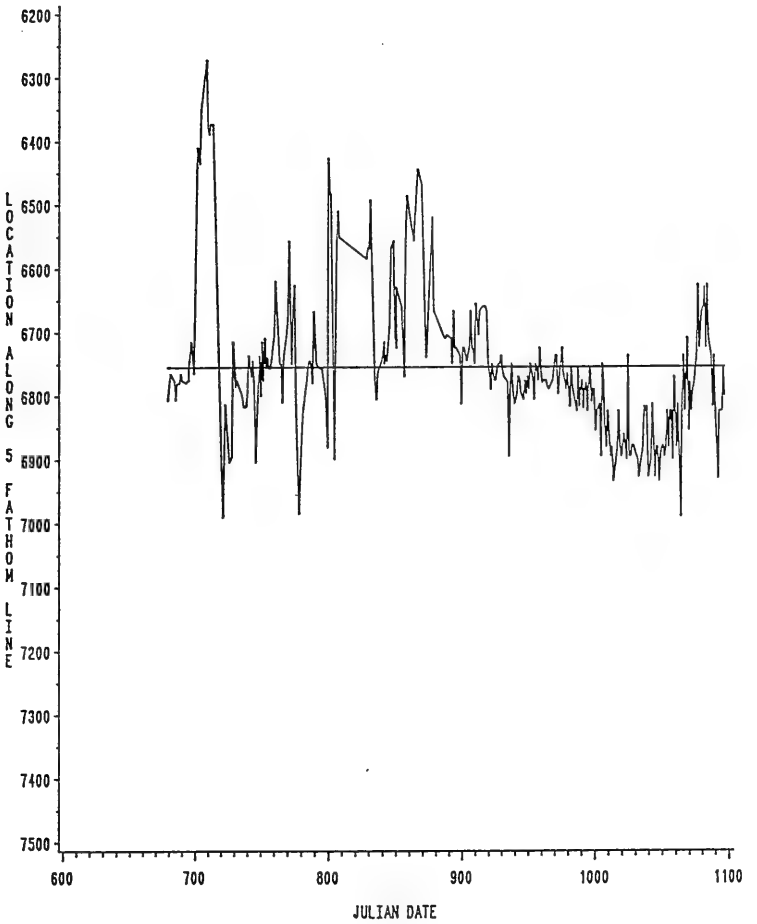


FIGURE 10.20a -- Daily locations of juvenile female California sea otter #35, as in Fig. 10.19a. Horizontal lines are the mean positions during arbitrary 30-day segments. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

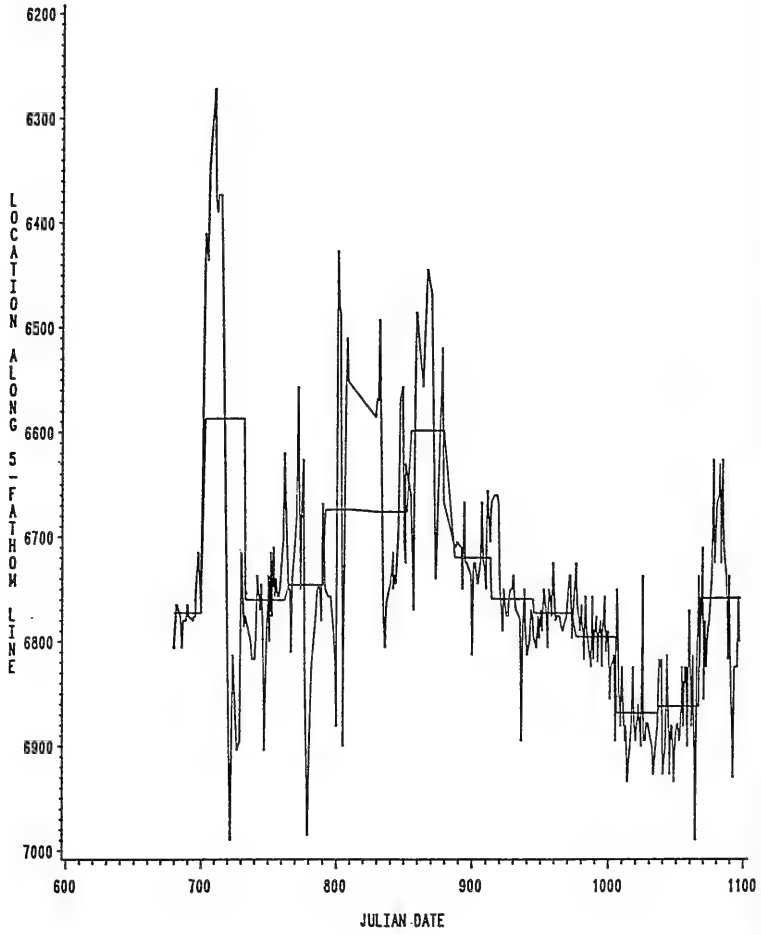
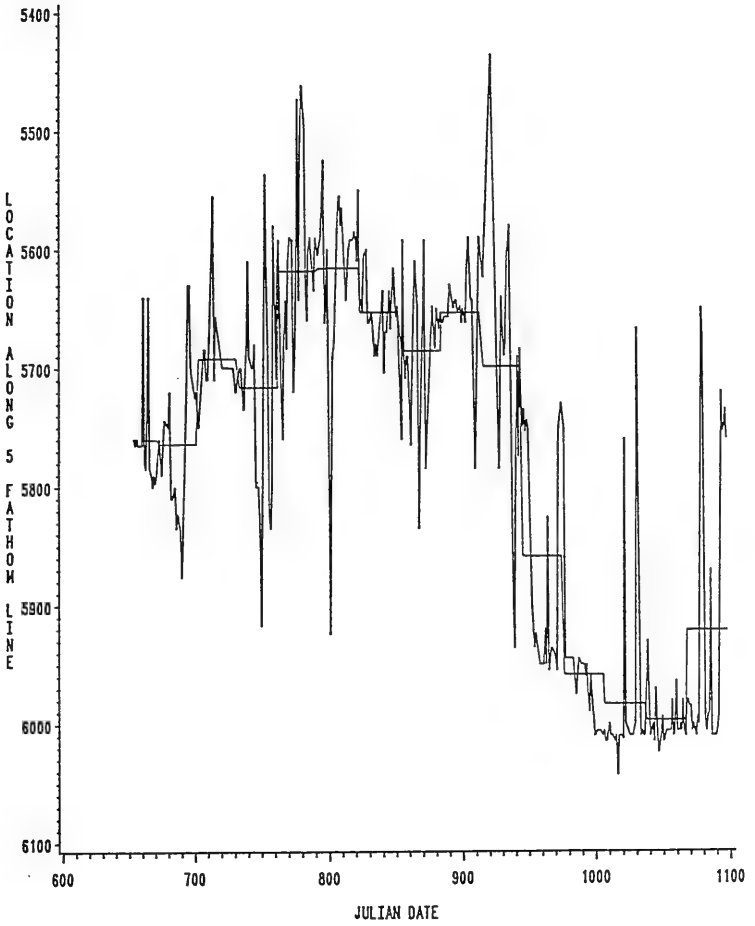


FIGURE 10.20b -- Daily locations of juvenile male California sea otter #29, as in Fig. 10.19b. Horizontal lines are the mean positions during arbitrary 30-day segments. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.



V_{max}, the maximum daily rate of travel was estimated for each class of animal by considering the maximum distance between locations taken at least 24 hours apart for each animal, and calculating maximum net daily movement:

$$V_{max} = MAX\{ \ |(d_x/d_h)|*24 \ \} \qquad (25)$$

where d_x is the distance between two successive locations and d_h is the time, in hours, between the locations. If an animal's class changed during the study periods of different classes were considered separately. These values were then grouped and averaged by class to get the values in Table 10.6. Since the greatest values of V_{max} are seen in juveniles (classes one and four), and it is unlikely that an otter's swimming speed decreases in adulthood, V_{max} for classes one-three is set equal to 48.6 500m segments/day in the model, and V_{max} for classes four and five is set equal to 37.5 500m segments/day. Pups likely restrict female movements, so V_{max} for class six animals remains at 8.4 500m segments/day in the model.

Table 10.6. Parameters used in short-term otter movement model. AR and CE are regression parameters discussed in text. sd is standard deviation of regression errors, R^2 given for regressions. Vmax is mean maximum daily movement, derivation discussed in text.

Class	Status	AR	CE	sd	(R^2)	V_{max}
1	Juvenile male	-0.045	-0.290	8.56	(0.13)	48.9
2	Adult non-territorial male	0.105	-0.815	4.64	(0.37)	40.2
3	Adult territorial male	0.042	-1.044	1.93	(0.43)	36.2
4	Juvenile female	0.367	-0.163	8.09	(0.10)	37.5
5	Adult female w/o pup	-0.025	-0.406	6.39	(0.21)	20.0
6	Adult female w/pup	-0.009	-0.706	2.95	(0.38)	8.4

Migratory movements by adult males.--The probabilities of migratory movements for males of class two and three are calculated using the data from Jameson (1987), as in the distribution model. Probabilities are calculated on a daily basis assuming a normal distribution of arrival and departure

times. Since Jameson (1987) gives mean date of territory arrival, calculation of the mean date upon which males leave for their territories requires consideration of the transit time to the territory. We have arbitrarily set that at three days, so that the mean date of departure for a territory is 19 May.

The dates given by Jameson are far enough apart that there is no overlap in simulated territory arrival and departure. The same caveats about the seasonality in male migratory movements that were mentioned in the discussion of OTDIST apply here. The same values of the territorial parameters that are set for OTDIST are used in OTMOVE; seasonality less pronounced than that described by Jameson (1987) and as indicated by our telemetry data, can be simulated by setting large standard deviations of arrival and departure dates.

Movements in response to oil spill.--The parameters PM, PA, and PE are delphic parameters; very little data from which to estimate their values are available. Costa and Kooyman (1982) found that otters oiled over 25% of their surface will die of hypothermia if not cleaned, suggesting that PM could be very high. Ford and Bonnell (1986) use values of 30%-90% as most likely mortality rates in their simulations, depending on the condition of the oil, but allowed the possibility of mortality varying between 10 and 100%. Siniff, et al., (1982) found that captive sea otters did not avoid areas of the holding tanks experimentally contaminated with oil, suggesting that PA, the probability of localized movements to avoid the spill, may be very low. It is also likely that PE, the probability of leaving the spill area to establish a new home range, is a good deal smaller than PA.

The values of these parameters are set by the user at runtime, facilitating evaluation of the relative importance of these parameters in determining the amount of mortality from a spill within the structure of the model. Additionally, the values of these parameters are set independently for each day of the spill, allowing consideration of the effects of weathering on oil (i.e., PM decreasing with time), or possibly learning on the part of the animals (i.e., PA increasing with time), or other scenarios. We anticipate that much of the model's usefulness will be due to its ability to simulate different oil spill response scenarios.

Fig. 10.21 traces simulated movements of otters in the vicinity of an oil spill presumed to occur on December 1, and lasting 15 days, at the southern end of the Monterey Bay and eastern side of the Monterey Peninsula. The rangewide population in these simulations was set at 1600 animals. In Fig. 10.21a all delphic parameters are set to 0.0, that is,

the spill has no effect on the animals' behavior, and the movements thus reflect a "normal" situation. In Fig 10.21b PM and PA were set to 0.8 for the duration of the spill, and PE was set to 0.5 for the duration; in Fig. 10.21c PM was set to 0.1 for the duration, PA was set to 0.5 for the duration, and PE was set to 0 for the duration. The same initial population and distribution, and the same random number seeds, were used in all 3 simulations.

MODEL OUTPUT

A log file, recording the user-input parameter settings, is generated each time the model is run. Six files of raw output data are written as the model runs. One contains the simulated population sizes for control runs (runs without introduction of oil spills), and one contains the simulated population sizes for runs with oil spills. In each of these the numbers of males, females, and pups are recorded once a year, at the end of the month in which the oil spill occurs. A third file records the numbers of oil spill-caused deaths by class (juvenile male, adult non-territorial male, etc.) and by day of spill. The fourth file records the total number of deaths of males, females, and pups due to the spill in each run. The fifth file records the total population size just prior to the spill, and the number of simulated years that pass before the population recovers to that size. The sixth file records the total reproductive value of the population just before and just after the spill. The reproductive value of a female is the relative number of female pups she is expected to wean during the remainder of her life. For a female of age x, Fisher (1930) and Wilson and Bossert (1971) give the formula for reproductive value (v_x):

$$v_x = (e^{-rx}/l_x) \quad e^{-ry} l_y m_y \quad ; \quad y=x,W \tag{26}$$

Fig. 10.22 illustrates the reproductive values of females under default parameter settings and a per capita population growth rate = 0. The total reproductive value of the population is:

$$v_T = \quad n_x v_x \quad ; \quad x=1,W \tag{27}$$

where n_x is the number of females of age x in the population. The reduction in total reproductive value may provide a measure of how the perturbations in age and sex structure of the population caused by an oil spill effect population recovery.

FIGURE 10.21a -- Simulated movements of sea otters around an oil spill in Monterey Bay beginning 1 December and lasting 15 days. Boxed area (heavy dark line) represents spill location, between Fort Ord (365) and Point Pinos (390). Each trace represents a different simulated individual otter. Total range wide population at the time of the spill was set at 1600; OTDIST positioned 56 animals in the area covered by the diagram but for clarity only 25 were chosen, at random, for representation. Movement parameter settings (see text) were PM=0.0, PA=0.0, PE=0.0, for all days of the spill, thus simulating no oil-caused mortality or effect on behavior. The relatively few numbers of animals at the north end of the diagram reflect the much lower density of otters in the sandy habitat of Monterey Bay relative to the rocky habitat of the Monterey Peninsula. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

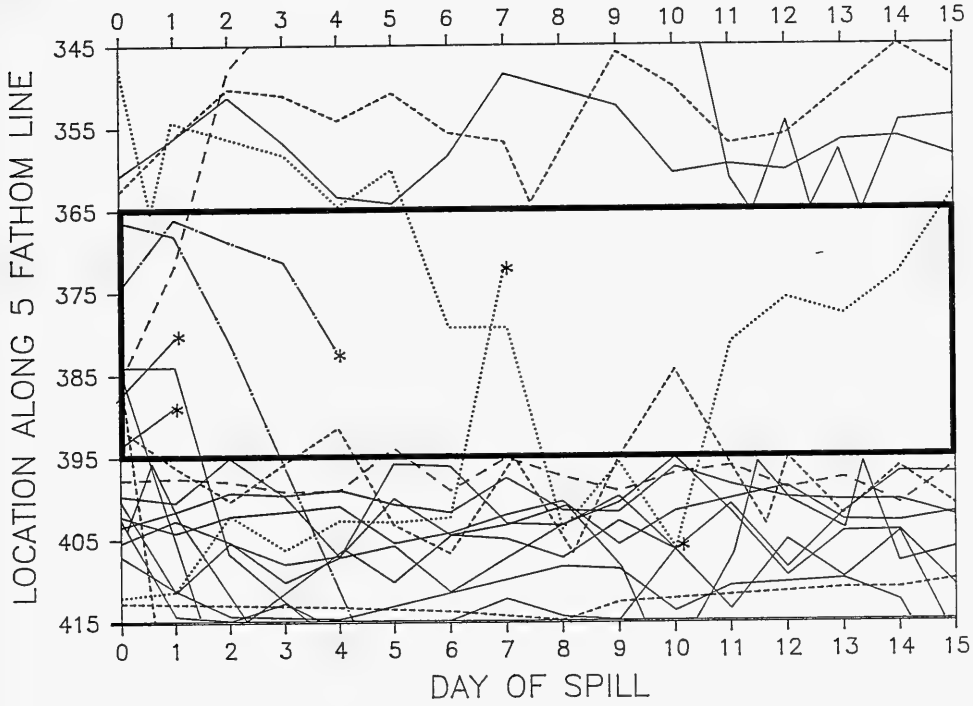


FIGURE 10.21b -- Simulated movements of sea otters around an oil spill in Monterey Bay beginning 1 December and lasting 15 days, as in Fig. 10.21a, except that in this simulation movement parameters were set at PM=0.8, PA=0.8, PE=0.5. A star (*) indicates an otter death. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

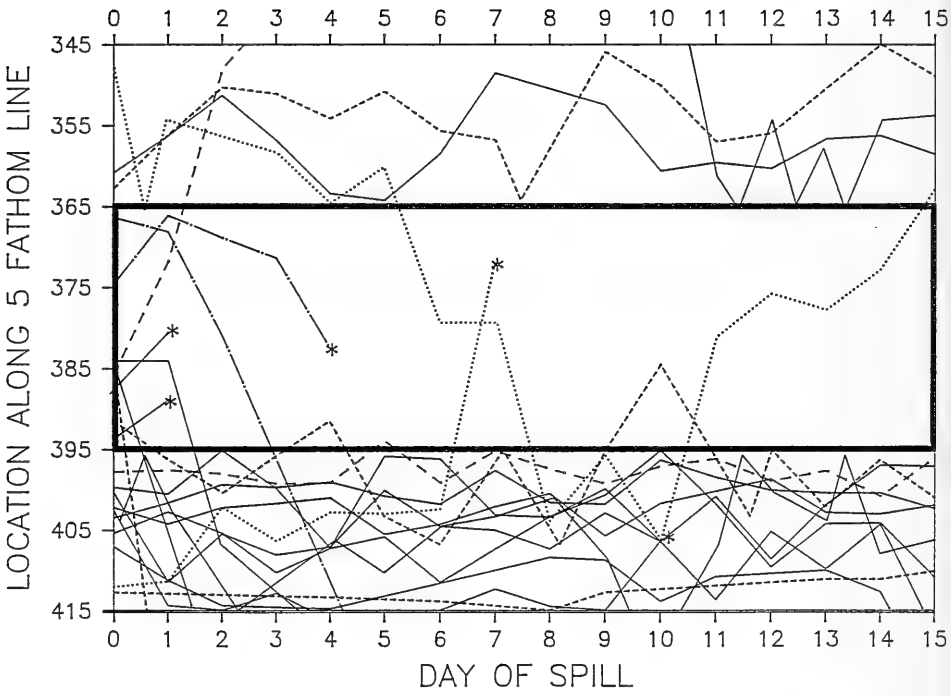


FIGURE 10.21c -- Simulated movements of sea otters around an oil spill in Monterey Bay beginning 1 December and lasting 15 days, as in Fig. 10.21a, except that in this simulation movement parameters were set at PM=0.1, PA=0.5, PE=0.0. A star (*) indicates an otter death. The numerical value of the locations along the five fathom line generally increases as one moves to the south along the California Coast.

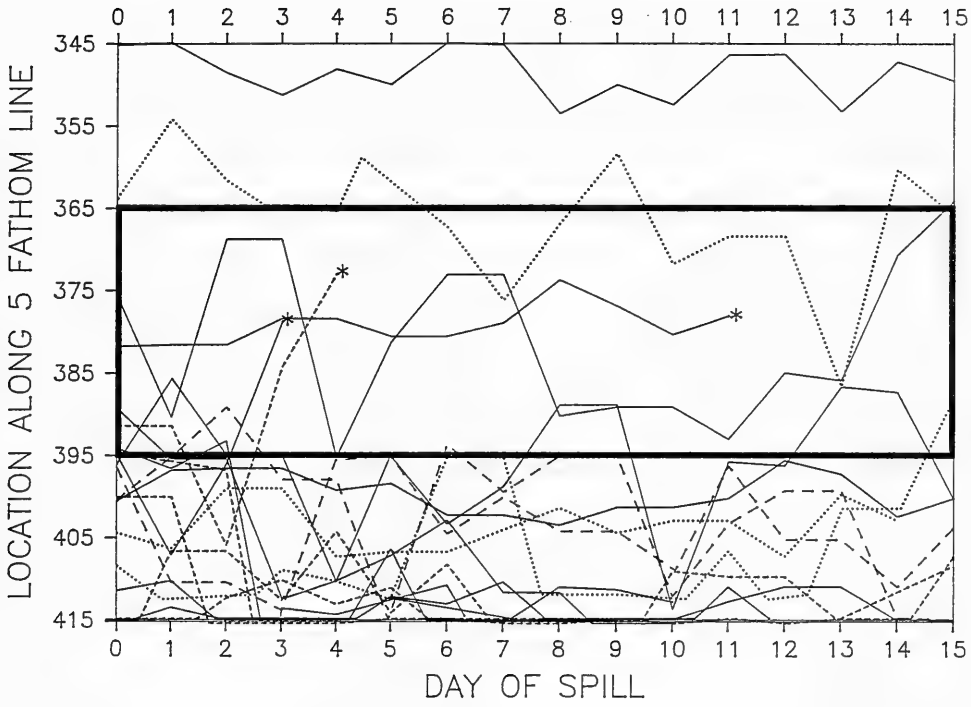
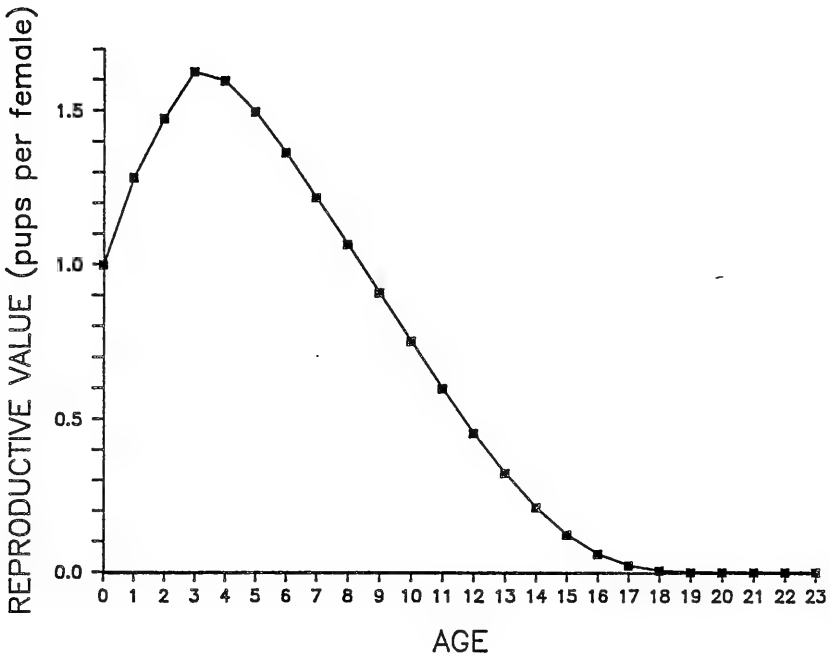


FIGURE 10.22 -- Age-specific reproductive values of female California sea otters under default parameter settings and a per capita growth rate=0.



A data summary and analysis program, OTPROC, has been written to summarize the raw output files and write a short report on the run. Additionally, OTPROC writes output files specifically designed to be read by LOTUS123. A LOTUS123 macro worksheet is supplied that will generate simple graphics illustrating the outcome of the model runs. Detailed discussion of the processing of model output can be found in the user's manual (Appendix 10.2). Examples of model output appear in Fig. 10.23.

OTRANGE

In an effort to be able to make predictions about the future status of the California sea otter population, and to aid in the estimation of some of the parameters used in OTPOP and LESLIE, we undertook an analysis and modeling of the historical growth of the population. Because of the type of data used and the speculative nature of the modeling, this work was conducted separately from the oil spill population model.

Background

The growth of the California sea otter population following almost complete elimination by the turn of the 20th century is described by CDFG (1976), Ralls, et al., (1983), and USFWS (1986). Information on the size and range of the population before 1968, when CDFG began intensive study of sea otters, is scanty and generally anecdotal. A remnant population of probably less than 100 individuals grew at what appeared to be a steady rate of approximately 5% per year until the mid 1970's, expanding the occupied range in the process. By 1969, when regular counts began, an estimated 1,390 otters inhabited the coast between Seaside and Point Estero. In 1976 the highest population estimate was recorded, 1,789 animals, and occupied range extended from Rio Del Mar to Pecho Rock. Population estimates have been relatively constant since 1976, while the range has continued to expand slightly.

Reasons for the arrest in population growth have been the subject of much debate centering around whether density dependent or density independent factors have been most influential in bringing about the decline. Miller (1980) maintained that the population had reached an equilibrium with habitat carrying capacity, and that starvation was the principal cause of mortality. Estes et al (1986), based on comparisons of time budgets with an Alaska population assumed to be food limited, concluded that the California population was not at carrying capacity, and that density independent processes, particularly accidental entanglement in fishing nets, were the primary factors limiting population growth.

FIGURE 10.23a - Log file from a run of the model. A large oil spill is introduced for 10 days beginning June 15 along the 50km section of coast between Marina and Yankee Point. Initial population size is set at 1600, carrying capacity set at 1600. See user's manual for explanation of parameters.

```
     DATE AND TIME USED TO GENERATE RANDOM NUMBER SEEDS
     20,"NUMBER OF YEARS PER RUN"
     100,"NUMBER OF RUNS WITH OIL SPILL"
     100,"NUMBER OF CONTROL RUNS"
     1600,"INITIAL POPULATION SIZE"
     6,"MONTH OF SPILL"
     15,"DAY OF SPILL"
     10,"DURATION OF SPILL"
     350,"NORTH BOUNDARY OF SPILL"
     450,"SOUTH BOUNDARY OF SPILL"
     1600,"EQUILIBRIUM POPULATION SIZE"
     201,"NORTH BOUNDARY OF RANGE"
     955,"SOUTH BOUNDARY OF RANGE"
     0.090,"MAXIMUM PER CAPITA ANNUAL GROWTH RATE"
     0.005,"NON-LINEARITY OF DENSITY DEPENDENCE"
     0.000,"DENSITY INDEPENDENT MORTALITY RATE"
     1.000,"DEGREE OF COMPENSATION"
     0.930,"ADULT FEMALE SURVIVAL RATE"
     15.000,"MODEL AGE OF FEMALE SENESCENCE"
     0.250,"PRIME REPRODUCTIVE RATE"
     0.530,"PUP SURVIVAL RATE"
     0.870,"ADULT MALE SURVIVAL RATE"
     9.000,"MODEL MALE AGE OF SENESCENCE"
     5.000,"PERCENT VARIATION IN ADULT SURVIVAL"
     5.000,"PERCENT VARIATION IN PUP SURVIVAL"
     "","AR","CE","SIGMA","VMAX"
     "JUVENILE FEMALES" 0.367-0.163 8.09037.500
     "ADULT FEMALES W/PUP"-0.025-0.406 6.39307.500
     "ADULT FEMALES W/O PUP"-0.009-0.706 2.950 8.400
     "JUVENILE MALES"-0.045-0.290 8.56048.900
     "ADULT NON-TERRITORIAL MALES" 0.105-0.815
   4.64048.900
     "ADULT TERRITORIAL MALES" 0.042-1.044 1.93048.900
     6,"AGE AT WHICH POTENTIALLY TERRITORIAL"
     60.000,"MAXIMUM % OF POTENTIALS THAT HOLD
     TERRITORIES"
     20.000,"MINIMUM % OF POTENTIALS THAT HOLD
     TERRITORIES"
     8.110,"MEAN TERRITORY LENGTH"
     0.440,"S.D. OF TERRITORY LENGTH"
     5,"MEAN ARRIVAL DATE MONTH"
     23,"MEAN ARRIVAL DATE DAY"
     11,"S.D. OF ARRIVAL DATE IN DAYS"
     12,"MEAN DEPARTURE DATE MONTH"
     1,"MEAN DEPARTURE DATE MONTH"
     15,"S.D. OF DEPARTURE DATE IN DAYS"
     "DAY",
   "P(MORTALITY)","P(AVOIDANCE)","P(EMIGRATION)"
```

TABLE 23a. (continued)

1	1.000	0.000	0.000
2	1.000	0.000	0.000
3	1.000	0.000	0.000
4	1.000	0.000	0.000
5	1.000	0.000	0.000
6	1.000	0.000	0.000
7	1.000	0.000	0.000
8	1.000	0.000	0.000
9	1.000	0.000	0.000
10	1.000	0.000	0.000

FIGURE 10.23b - Report file generated by OTPROC after the run in Fig. 10.23a.

CONTROL RUNS:

YEAR	FEMALES	MALES	PUPS
-4	1038.0(1038-1038, 0.0)	566.0(566-566, 0.0)	195.5(175-220, 10.7)
-3	1029.8(997-1064, 13.6)	559.4(529-589, 12.8)	244.8(220-272, 11.8)
-2	1047.1(1002-1105, 17.7)	579.5(529-615, 18.4)	228.5(193-262, 12.3)
-1	1056.4(1015-1110, 18.6)	590.6(542-632, 19.3)	215.4(170-248, 13.8)
0	1058.1(1002-1123, 24.7)	597.0(536-652, 20.9)	214.3(185-239, 12.6)
1	1035.7(979-1094, 23.4)	603.6(560-658, 20.0)	212.5(177-248, 12.9)
2	1021.3(978-1066, 1938)	606.9(558-650, 18.2)	213.8(181-249, 14.5)
3	997.1(916-1049, 22.2)	593.9(526-645, 21.0)	214.7(188-238, 9.5)
4	997.9(938-1063, 24.7)	582.2(520-640, 24.5)	211.0(167-240, 11.1)
5	998.8(935-1058, 23.1)	573.3(509-628, 23.8)	208.8(189-235, 9.2)
6	1007.0(947-1071, 23.3)	568.7(506-623, 24.6)	207.6(175-234, 10.9)
7	1010.4(947-1074, 25.0)	563.4(508-627, 22.9)	210.9(186-238, 10.7)
8	1018.3(955-1084, 25.5)	559.8(504-619, 23.3)	213.1(190-245, 11.3)
9	1026.5(969-1085, 24.7)	558.3(507-615, 24.4)	215.2(183-250, 12.9)
10	1031.2(965-1090, 27.3)	557.3(499-627, 26.6)	216.7(179-244, 11.1)
11	1037.4(973-1098, 27.3)	555.8(508-623, 25.8)	219.1(194-242, 11.4)
12	1038.5(980-1103, 28.4)	558.0(484-617, 24.6)	220.9(187-255, 10.3)
13	1039.4(964-1136, 28.1)	560.9(508-622, 21.1)	219.8(196-241, 9.9)
14	1039.3(965-1115, 26.0)	564.7(494-619, 21.6)	220.2(201-246, 9.4)
15	1039.2(980-1086, 23.1)	565.9(512-616, 21.2)	219.5(200-250, 9.9)
16	1036.3(976-1103, 23.3)	565.3(516-618, 21.8)	220.9(186-254, 12.2)
17	1034.8(972-1091, 23.4)	565.8(503-623, 23.4)	220.3(188-240, 11.2)
18	1039.0(988-1108, 24.0)	565.9(510-636, 23.8)	218.2(190-248, 11.1)
19	1034.8(975-1109, 25.6)	564.6(518-642, 22.6)	219.1(191-250, 11.0)
20	1032.3(966-1081, 23.8)	564.9(506-616, 23.0)	219.4(195-250, 10.6)

FIGURE 10.23b (continued)

OIL SPILL RUNS:

YEAR	FEMALES	MALES	PUPS
-4	1038.0 (1038-1038, 0.0)	566.0(566-566, 0.0)	196.4(165-217,11.1)
-3	1030.4 (955-1061,13.0)	559.1(530-589,12.9)	232.7(195-277,16.0)
-2	1044.0 (983-1090,19.3)	573.5(531-617,18.8)	219.0(188-254,16.0)
-1	1049.3 (978-1108,26.3)	585.2(531-624,21.2)	211.5(187-251,13.3)
-0	1047.4 (972-1116,29.8)	590.2(541-652,24.2)	211.0(180-251,12.5)
+0	785.3 (713- 860,29.4)	558.1(508-612,23.9)	162.6(134-194,11.8)
1	837.5 (740- 899,31.5)	540.3(472-612,26.3)	169.6(140-208,12.9)
2	887.3 (784- 949,28.7)	530.0(468-609,28.6)	176.0(151-205,12.7)
3	923.5 (836- 984,27.4)	515.4(462-575,26.6)	181.3(150-201,10.3)
4	956.7 (884-1019,26.6)	501.0(440-563,27.2)	188.4(157-210,11.4)
5	989.5 (894-1048,28.0)	496.4(418-566,25.0)	197.1(169-230,10.5)
6	1019.8 (933-1085,26.6)	496.0(431-571,24.8)	206.1(178-231,10.6)
7	1045.6 (983-1119,26.2)	500.7(435-579,25.9)	214.3(186-241,11.6)
8	1063.4 (1008-1128,23.5)	512.8(453-582,24.3)	221.0(200-244,10.5)
9	1073.8 (1029-1135,22.3)	527.7(458-578,25.6)	227.6(204-255,10.9)
10	1077.9 (1022-1146,26.2)	542.5(490-615,24.2)	229.9(201-259,10.5)
11	1068.6 (1011-1124,24.4)	556.1(511-608,23.8)	230.1(196-263,12.3)
12	1060.1 (968-1110,27.7)	567.4(519-634,23.5)	228.4(189-258,12.5)
13	1047.4 (963-1107,25.8)	574.8(519-643,24.6)	227.4(202-265,11.8)
14	1039.0 (973-1111,24.3)	578.6(531-638,24.6)	225.5(189-262,11.5)
15	1033.9 (972-1096,27.9)	579.1(528-666,27.4)	223.3(200-256,10.7)
16	1027.7 (924-1101,27.8)	578.6(532-638,24.5)	219.4(196-246,11.1)
17	1025.3 (896-1132,29.6)	577.4(520-642,22.8)	215.2(184-252,11.7)
18	1020.4 (892-1088,27.2)	572.3(524-619,22.3)	215.4(166-238,11.4)
19	1018.4 (902-1082,28.3)	568.3(514-628,23.8)	214.0(165-241,11.0)
20	1021.8 (956-1075,24.7)	568.1(511-626,25.1)	213.7(188-240,10.7)

NUMBER OF DEATHS FROM OIL SPILL:

				PERCENT OF POPULATION			
CLASS	MEAN	S.D.	RANGE	MEAN	S.D.	RANGE	
JUVENILE MALES	13.4	4.0	5 - 25	4.96	1.48	1.90	7.90
ADULT MALES	18.7	3.2	12 - 29	5.86	1.01	3.40	8.90
JUVENILE FEMALES	75.7	8.3	60 - 100	26.88	2.65	22.00	37.20
ADULT FEMALES	186.4	12.1	160 - 222	24.35	1.58	20.80	29.40
PUPS	48.4	6.6	33 - 67	22.95	2.94	15.20	32.00
TOTAL ANIMALS	342.5	19.0	304 - 383	18.54	1.06	16.20	21.00

RECOVERY AFTER OIL SPILL:

	MEAN	S.D.	RANGE
REPRODUCTIVE VALUE BEFORE SPILL	1316.3	39.5	1223.2-1409.9
REPRODUCTIVE VALUE AFTER SPILL	987.7	39.4	889.9-1073.3
REDUCTION (%)	24.971	1.52641	22.271-28.831
YEARS TO RECOVERY	9.800	1.71270	7.000-17.000

**ON 25 OF 100 RUNS (25.0%) THE POPULATION DID NOT RECOVER TO PRE-SPILL SIZE

TIME TO RECOVERY CALCULATED ONLY FOR RUNS THAT DID RECOVER.

FIGURE 10.23c -- Trace of the total simulated population size for runs in Fig. 10.23a. Mean and range of 100 runs. Oil spill occurs at year 0.

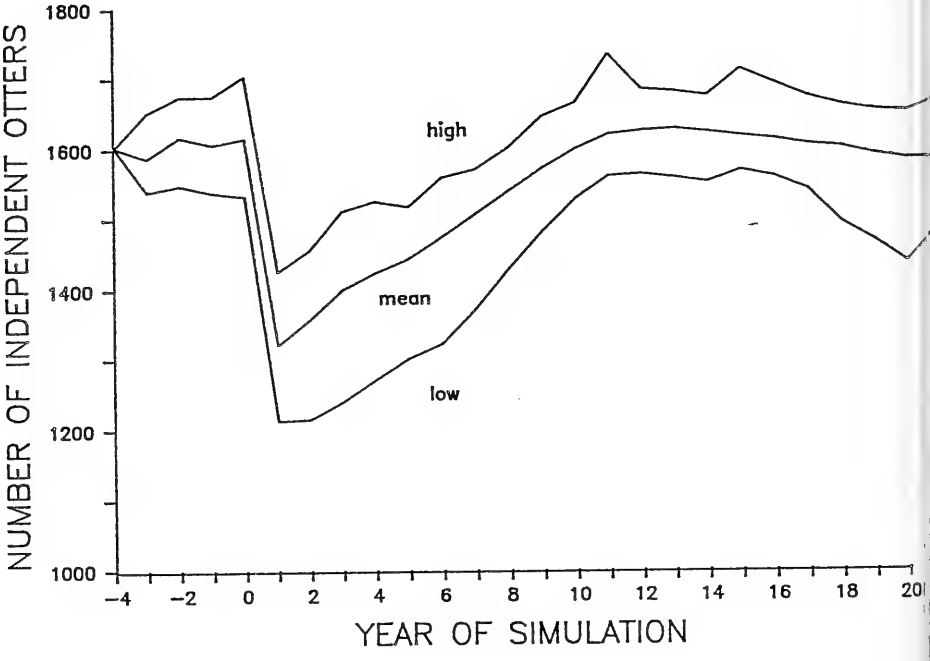


FIGURE 10.23d -- Trace of the total simulated population size for the control (no oil spill) runs in Fig. 10.23a. Mean and range of 100 runs.

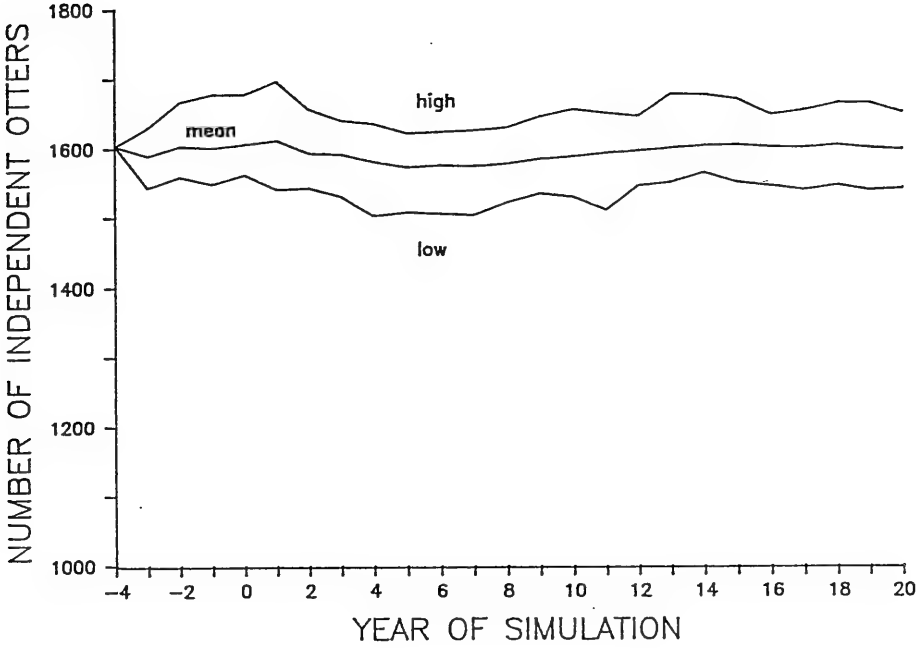


FIGURE 10.23e -- Trace comparing the mean values from Figs. 10.23c and 10.23d.

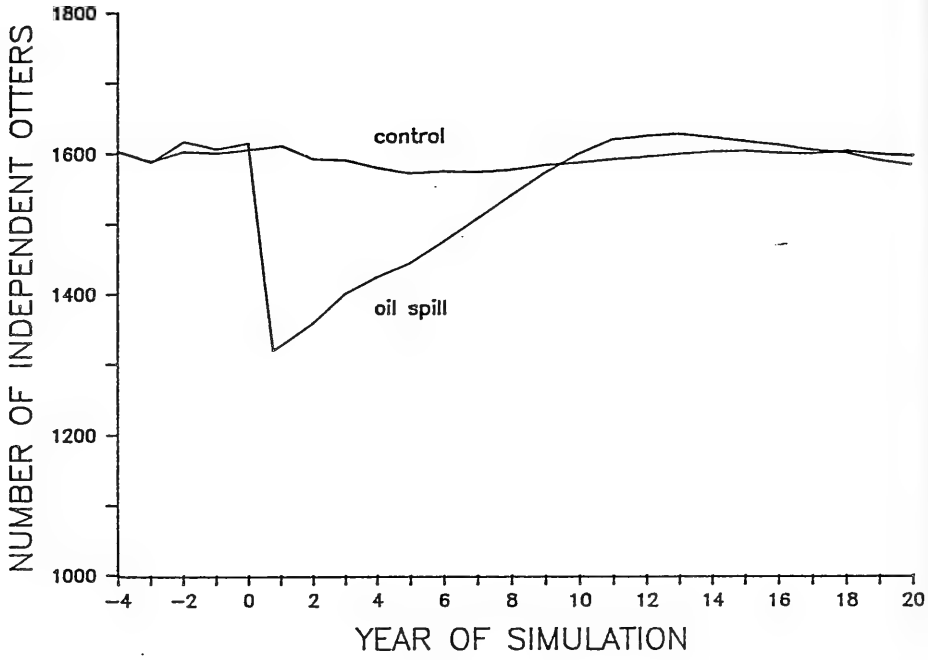
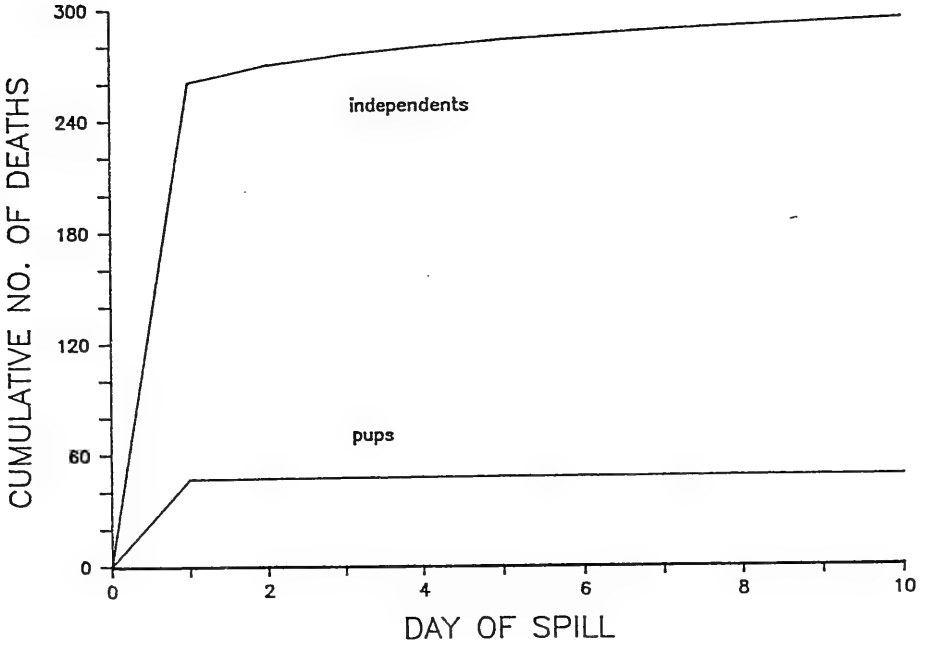


FIGURE 10.23f -- Mean cumulative number of otter deaths due to oiling for the run in Fig. 10.23a.



Relatively high levels of commercial gill- and trammel-net fishing along the central coast began in the early 1970's, coincident with the decline in sea otter population growth. Wendell, et al., (1985) estimated that approximately 80 sea otters drowned accidentally in nets each year between 1973 and 1983. Ames, et al., (1985) suggested that density dependent processes are most important in the central part of the range, where the population has been established for the longest period of time and has depressed prey populations below pre-recolonization levels, while at the range peripheries, which still have relatively low numbers of otters, density independent processes, particularly accidental entanglement and great white shark attacks are the most important factors limiting the growth of the population. The time budget data we gathered using telemetry in areas of the central part of the range tended to support the suggestion that the juvenile females may be suffering from food limitations in the central part of the range (see Chapter 4), but the evidence is not conclusive and does not address the situation at the range peripheries.

The degree of density dependence in the dynamics of a particular population is a question that must be addressed by any attempt to model that population. The uncertainty surrounding this issue in the California sea otter population led us to build in to our model the capability of simulating any degree of density dependence. This approach allows simulation of the effect of oil spills under different conceptual hypotheses about the dynamics of the population, but does little towards providing a set of parameters most applicable to a timely and realistic risk analysis. In an effort to better understand the dynamics and estimate pertinent parameters we have attempted to simulate the historical growth of the California population with a model (OTRANGE) that incorporates a feedback mechanism between population size and range size. It is hoped that a model that fits the historical data will be of value in predicting future population sizes and range extent. Because of the speculative nature of the mechanisms incorporated in the model, and the amount of computer time required to fit model parameters to the historical data, OTRANGE is completely deterministic. It is intended only as an aid in determining the values of user-input parameters in the main risk analysis model, particularly when considering spills in the future.

Structure

The density dependence function used in the population dynamics portion of OTRANGE is the same as that used in OTPOP and LESLIE (eq. (3), Fig. 10.4, and Fig. 10.25). Range expansion is incorporated with the assumption that range expansion is density dependent, and that range expansion

results in an increased population-wide carrying capacity (Fig. 10.24). Biologically, this means that as the population approaches its carrying capacity it can respond by both reducing its growth rate, and by increasing its carrying capacity through an increase in the area of occupied habitat. The density dependence function for range size is simply taken as the mirror image of the density dependence function for population size (Fig. 10.25):

$$k = k_{max} - k_{max}\{1-\exp\{-b(K-N)]\} \quad (27)$$

where k is the annual rate of change in carrying capacity, k_{max} is the maximum annual rate of change of k, K is the carrying capacity, N is the population size, and b governs the shape of the curve. As in the population dynamics portion of the model, an arbitrary ceiling on the size of k is imposed at k_{max}.

The fact that occupied range has expanded faster to the south than to the north, and the fact that the range continued to expand during the period of apparent population decline in the late 1970,s, led us to modify (27) in the model. First, range expansion to the north and to the south are considered separately. Secondly, allowance is made for density independent range expansion. Biologically, density independent range expansion may be the result of natural dispersal of young animals, regardless of the equilibrium status of the population, superimposed on a limited geographic range. OTRANGE thus uses

$$k_s = k_{d,s} + k_{max,s} - k_{max,s}\{1-\exp\{-b(K-N)]\} \quad \text{and}$$
$$k_n = k_{d,n} + k_{max,n} - k_{max,n}\{1-\exp\{-b(K-N)]\} \quad (28)$$

where k_s and k_n are annual range expansion rates to the south and to the north, respectively, $k_{d,s}$ and $k_{d,n}$ are density independent rates of range expansion to the south and to the north respectively, $k_{max,s}$ and $k_{max,n}$ are the maximum rates of range expansion to the south and to the north, respectively, and b, K, and N are as in (27).

Translating k, which is terms of numbers of animals, into range size requires an estimate of the number of animals that can be supported in a given area of habitat. Ford and Bonnell (1986), using USFWS census data, estimated that maximal densities were 4.7 otters per km^2 over rocky substrate and 1.3 otters per km_2 over sandy substrate. By digitizing the coast, assuming that otter habitat extended from the coast to the 20

FIGURE 10.24 -- Schematic representation of OTRANGE. At each iteration, the quantity K-N determines the next iteration's population size and carrying capacity.

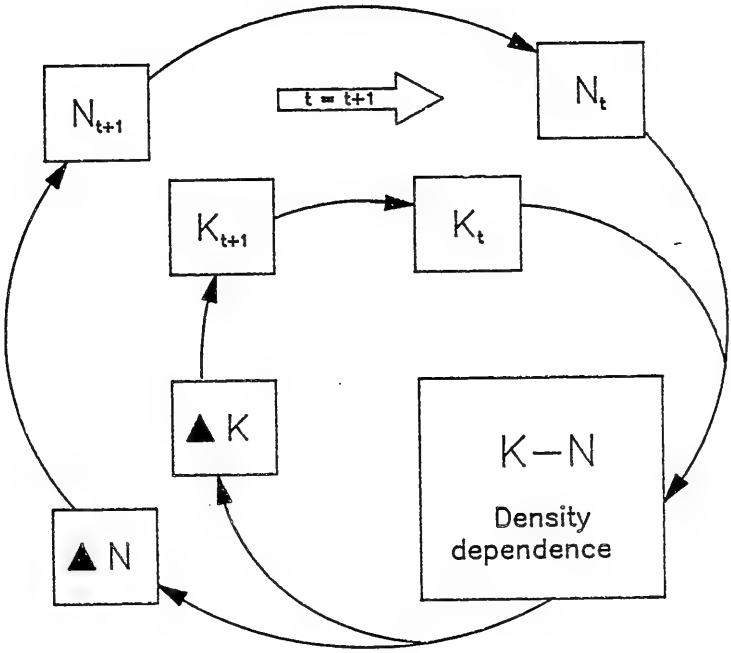
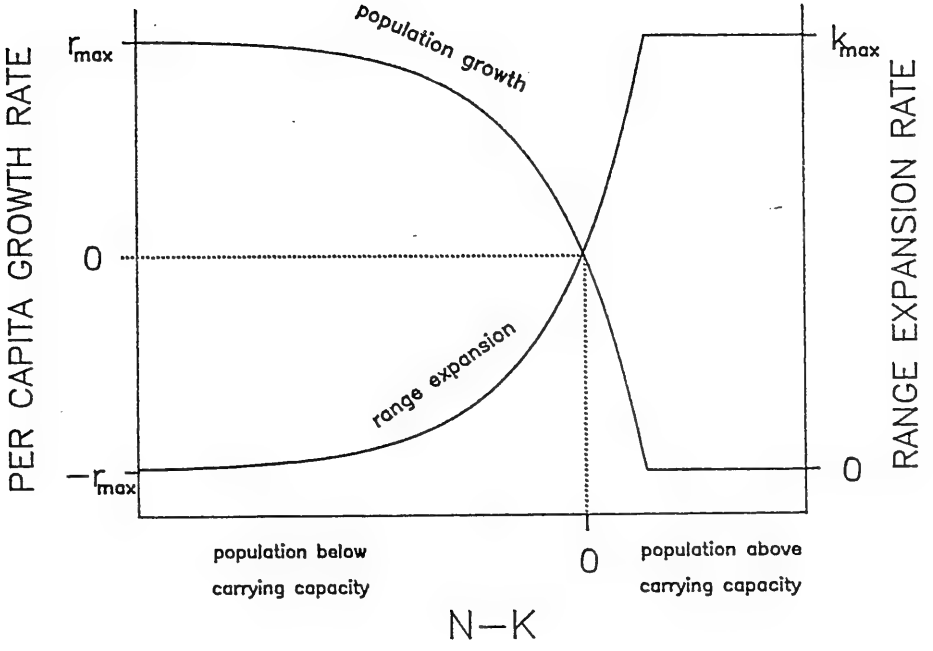


FIGURE 10.25 -- Density dependence functions used in OTRANGE. The parameter b affects the shape of the curve (see Fig. 10.4).



fathom depth contour, coding substrate from USGS maps, and using Ford and Bonnell's (1986) estimates, we calculated the carrying capacity of each 0.5 km segment of the 5 fathom line ordinate system. This allowed calculation of historical values of K given the length of occupied range at any point in the past. Using the historical range length data in USFWS (1986, Table 1.3) we calculated historical carrying capacities based on Ford and Bonnell's (1986) estimates. The calculated carrying capacities were well below historical population estimates, leading us to believe that Ford and Bonnell's census-based estimates underestimated actual carrying capacity, and forcing us to include the per hectare carrying capacities of rock and sand substrates in the group of parameters to be estimated.

Parameterization

We estimated OTRANGE parameters by means of a 2-stage numerical search. First, we chose what seemed to be reasonable bounds on the value of each parameter in the model, and a testing interval for each parameter between those bounds. Then the model was run under every possible combination of parameter values within the bounds, using the 1914 historical estimates of population size and carrying capacity as initial conditions. Goodness of fit to historical data was calculated for each run by comparing the modeled population size and range-wide carrying capacity to the historical estimates of those values for each year that historical data were available. Total sum of squares of the difference between the modeled and historical values was the goodness of fit criterion.

A total of over 196,000 combinations of parameter values were tested in the first stage of estimation. The 20 parameter combinations that gave the best fit to the historical data by each of the goodness of fit criteria were saved, new bounds chosen from those combinations, and the analysis repeated with a smaller testing interval for each parameter. Over 40,000 parameter combinations were tested in this second stage of estimation. The parameter combination that gave the best fit is listed in Table 10.7, and a trace of the model run under this parameterization is shown in Fig. 10.26.

Table 10.7. Parameters giving the best fit of OTRANGE to historical data. See text for explanation of parameters.

Parameter	OTRANGE without density independent mortality	OTRANGE with density independent mortality
Maximum per capita growth rate (r_{max})	0.085	0.077
Non-linearity of density dependence (b)	0.020	0.030
Maximum density dependent rate of expansion:		
North($k_{max,n}$):	7.5	8.5
South($k_{max,s}$):	20.7	27.5
Density independent rate of expansion:		
North($k_{d,n}$):	8.0	2.6
South($k_{d,s}$):	10.0	13.5
Per hectare carrying capacity		
Rock substrate:	0.26	6.5
Sand substrate:	0.78	6.75
Density independent mortality rate (m)	--	0.03

Incorporation of density independent mortality.

The parameterization of the above model that produced the best fit to the historical data produced oscillations in population size once the population approached 1600 animals. This may imply that the stabilization of population size that occurred in the mid-1970's is a consequence of the internal dynamics of the population and its habitat, and that stabilization would have occurred even without gill net mortality. In other words, it implies that gill-net mortality completely compensates for natural mortality, and that if animals would not have been killed in the nets they would have died from natural causes. Certainly natural mortality is greater than 5% per year (see Figs. 10.7,10.9, and 10.10), and compensatory density independent mortality of the magnitude due to gill-nets is mathematically possible.

We decided to investigate the possibility that gill-net mortality is completely additive to natural mortality. We thus modified the population growth equation:

$$r = r_{max}\{1-\exp[-b(K-N)]\}-m \qquad (29)$$

where m is the density independent mortality rate. We then estimated parameters in the same manner as above, including

FIGURE 10.26 -- Fit of OTRANGE output to historical data using the parameters in Table 10.7 without density independent mortality. Solid line traces population size, dashed line traces carrying capacity.

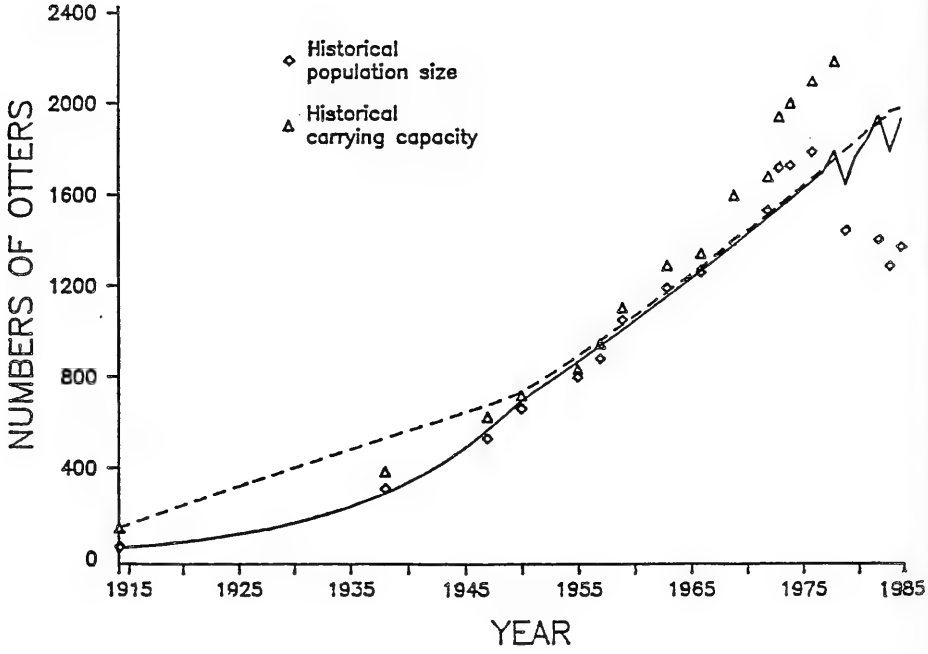
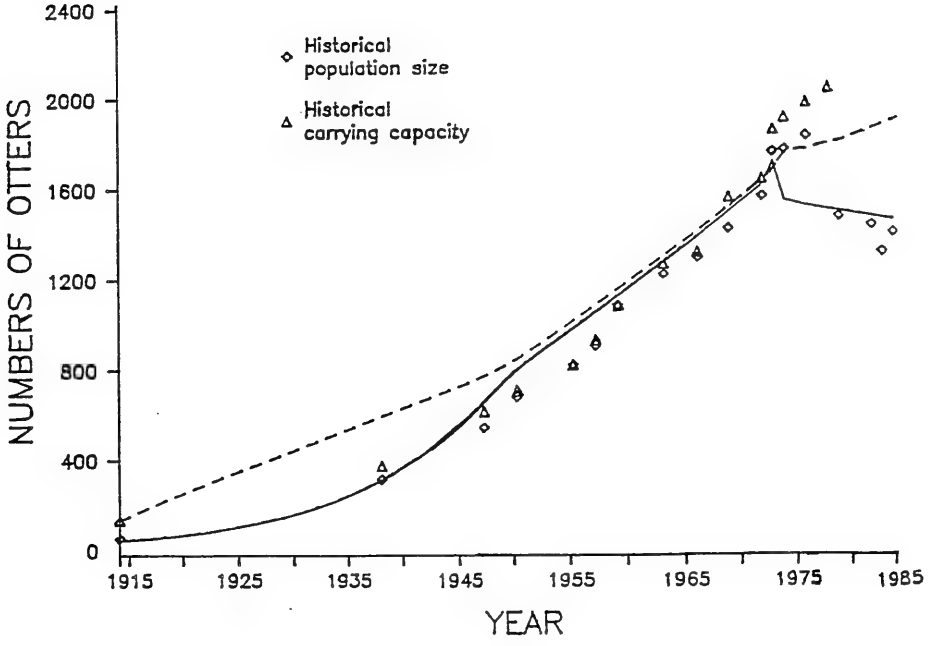


FIGURE 10.27 -- Fit of OTRANGE output to historical data using the parameters in Table 10.7 incorporating density independent mortality. Solid line traces population size, dashed line traces carrying capacity.



m in the list of parameters that were estimated. Density independent mortality was incorporated in the model only after 1972, to simulate the effect of gill-net mortality. A trace of the simulated dynamics that produced the best fit appears in Fig. 10.27.

Caveats

The model incorporating density independent mortality produced a better fit to the historical data than did the basic model (total sum of squares =870,616 vs. 1,121,621). In the parameterization giving the best fit, m =0.03, less than the 5% gill net mortality estimated by Wendell et al (1985), perhaps indicating that gill net mortality is partly compensatory.

Neither of the models fits the historical data particularly well, and there is no guarantee that the mechanisms in the model mimic those in the natural population. There are two levels on which our approach should be criticized. First, we made no effort to investigate different functional forms of density dependent range expansion. As far as we know no other attempts have been made to model density-dependent changes in carrying capacity in any situation; we did not have the advantage of theoretical precedents. We used the mirror image of the population growth function as a convenient starting point, but there is no reason to assume that it is correct. Secondly, of course, parameter estimates are only as good as the data they are based on. For example, Geibel and Miller (1980) and Wendell, et al., (1986) described the problems associated with the estimation of sea otter population size.

Relationship between OTRANGE and OTPOP

The analysis of OTRANGE under different parameterizations gave the default parameter values for r_{max}, b, and K used in OTPOP and LESLIE (Table 10.2). Because the proposed oil and gas developments that are of concern will not occur until the 1990's, at the earliest, and because much of that development is proposed for what is now peripheral to occupied sea otter range, we have supplied OTRANGE to MMS in a form that can be used to predict future population size, range size, and carrying capacity. These predictions can then be used as input to the main model to simulate initial conditions in the future.

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APPENDICES

Appendix 2.1 - Reproductive data on individual females.

SEA OTTER 6

DATE	DAYS BETWEEN	CUM DAYS	STATUS
05-JUL-84			NO PUP
07-JUL-84	2	2	NO PUP
08-JUL-84	1	3	NO PUP
17-JUL-84	9	12	NO PUP
18-JUL-84	1	13	NO PUP
19-JUL-84	1	14	NO PUP
21-Jul-84	2	16	NO PUP
22-Jul-84	1	17	NO PUP
23-Jul-84	1	18	NO PUP
25-Jul-84	2	20	NO PUP
26-Jul-84	1	21	NO PUP
27-Jul-84	1	22	NO PUP
28-Jul-84	1	23	NO PUP
29-Jul-84	1	24	NO PUP
30-Jul-84	1	25	NO PUP
08-Aug-84	9	34	NO PUP
13-Aug-84	5	39	NO PUP
21-Aug-84	8	47	NO PUP
31-Aug-84	10	57	NO PUP
01-Sep-84	1	58	NO PUP
01-Sep-84	0	58	NO PUP
02-Sep-84	1	59	NO PUP
03-Sep-84	1	60	NO PUP
05-Sep-84	2	62	NO PUP
06-Sep-84	1	63	NO PUP
08-Sep-84	2	65	NO PUP
12-Sep-84	4	69	NO PUP
15-Sep-84	3	72	NO PUP
17-Sep-84	2	74	NO PUP
14-Nov-84	58	132	NO PUP
29-Nov-84	15	147	NO PUP
21-Dec-84	22	169	NO PUP
26-Dec-84	5	174	NO PUP
15-Jan-85	20	194	NO PUP
20-Feb-85	36	230	NO PUP
21-Feb-85	1	231	NO PUP
06-Mar-85	13	244	NO PUP
12-Mar-85	6	250	NO PUP
13-Mar-85	1	251	NO PUP
14-Mar-85	1	252	NO PUP
02-Apr-85	19	271	NO PUP
16-Apr-85	14	285	NO PUP
18-Apr-85	2	287	NO PUP
02-May-85	14	301	NO PUP
11-Jun-85	40	341	NO PUP
21-Jun-85	10	351	NO PUP

SEA OTTER 9

DATE	DAYS BETWEEN	CUM DAYS	STATUS
02-Mar-85			
07-Mar-85	5	5	NO PUP
08-Mar-85	1	6	NO PUP
19-Mar-85	11	17	NO PUP
01-Apr-85	13	30	NO PUP
02-Apr-85	1	31	NO PUP
11-Apr-85	9	40	NO PUP
15-Apr-85	4	44	NO PUP
20-Apr-85	5	49	NO PUP
22-Apr-85	2	51	NO PUP
23-Apr-85	1	52	NO PUP
04-May-85	11	63	NO PUP
05-May-85	1	64	NO PUP
07-May-85	2	66	NO PUP
15-May-85	8	74	NO PUP
16-May-85	1	75	NO PUP
17-May-85	1	76	NO PUP
28-May-85	11	87	NO PUP
10-Jun-85	13	100	NO PUP
23-Jun-85	13	113	PUP
24-Jun-85	1	114	PUP
25-Jun-85	1	115	PUP
27-Jun-85	2	117	PUP
29-Jun-85	2	119	PUP
02-Jul-85	3	122	PUP
03-Jul-85	1	123	PUP
20-Jul-85	17	140	PUP
29-Jul-85	9	149	PUP
09-Aug-85	11	160	NO PUP
12-Aug-85	3	163	NO PUP
15-Aug-85	3	166	NO PUP
16-Aug-85	1	167	NO PUP
23-Aug-85	7	174	NO PUP
24-Aug-85	1	175	NO PUP
03-Sep-85	10	185	NO PUP
04-Sep-85	1	186	NO PUP
06-Sep-85	2	188	NO PUP
12-Sep-85	6	194	NO PUP
07-Oct-85	25	219	NO PUP
23-Oct-85	16	235	NO PUP
31-Oct-85	8	243	NO PUP
15-Nov-85	15	258	NO PUP
12-Dec-85	27	285	NO PUP
15-Dec-85	3	288	NO PUP
08-Jan-86	24	312	NO PUP
10-Jan-86	2	314	NO PUP

SEA OTTER 9 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
14-Jan-86	4	318	NO PUP
23-Jan-86	9	327	NO PUP
05-Feb-86	13	340	NO PUP
08-Feb-86	3	343	NO PUP
10-Feb-86	2	345	NO PUP
13-Feb-86	3	348	NO PUP
06-Mar-86	21	369	NO PUP
17-Mar-86	11	380	NO PUP
29-Mar-86	12	392	NO PUP
18-Apr-86	20	412	NO PUP
14-May-86	26	438	NO PUP
18-Jun-86	35	473	NO PUP
05-Jul-86	17	490	NO PUP
25-Aug-86	51	541	PUP

SEA OTTER 11

DATE	DAYS BETWEEN	CUM DAYS	STATUS
17-May-85			NO PUP
07-Sep-85	113	113	PUP
22-Jul-86	318	431	NO PUP

SEA OTTER 14

DATE	DAYS BETWEEN	CUM DAYS	STATUS
18-Mar-85			NO PUP
19-Mar-85	1	1	NO PUP
20-Mar-85	1	2	NO PUP
27-Mar-85	7	9	NO PUP
02-Apr-85	6	15	NO PUP
08-Apr-85	6	21	NO PUP
14-Apr-85	6	27	NO PUP
20-Apr-85	6	33	NO PUP
21-Apr-85	1	34	NO PUP
22-Apr-85	1	35	NO PUP
01-May-85	9	44	NO PUP
14-May-85	13	57	NO PUP
14-May-85	0	57	NO PUP
14-May-85	0	57	NO PUP
15-May-85	1	58	NO PUP
15-May-85	0	58	NO PUP
16-May-85	1	59	NO PUP
18-May-85	2	61	NO PUP
28-May-85	10	71	NO PUP
10-Jun-85	13	84	NO PUP
12-Jun-85	2	86	NO PUP
23-Jun-85	11	97	PUP
24-Jun-85	1	98	PUP
25-Jun-85	1	99	PUP
29-Jun-85	4	103	PUP
01-Jul-85	2	105	PUP
02-Jul-85	1	106	PUP
03-Jul-85	1	107	PUP
20-Jul-85	17	124	PUP
27-Jul-85	7	131	PUP
29-Jul-85	2	133	PUP
05-Aug-85	7	140	PUP
12-Aug-85	7	147	PUP
15-Aug-85	3	150	PUP
16-Aug-85	1	151	PUP
20-Aug-85	4	155	PUP
22-Aug-85	2	157	PUP
23-Aug-85	1	158	PUP
24-Aug-85	1	159	PUP
27-Aug-85	3	162	PUP
31-Aug-85	4	166	PUP
01-Sep-85	1	167	PUP
04-Sep-85	3	170	PUP
05-Sep-85	1	171	PUP
06-Sep-85	1	172	PUP
10-Sep-85	4	176	PUP
11-Sep-85	1	177	PUP

SEA OTTER 14 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
19-Sep-85	8	185	PUP
25-Sep-85	6	191	PUP
30-Sep-85	5	196	PUP
23-Oct-85	23	219	PUP
28-Oct-85	5	224	PUP
31-Oct-85	3	227	PUP
15-Nov-85	15	242	PUP
19-Nov-85	4	246	PUP
09-Dec-85	20	266	NO PUP
10-Dec-85	1	267	NO PUP
14-Dec-85	4	271	NO PUP
28-Dec-85	14	285	NO PUP
18-Jan-86	21	306	NO PUP
29-Jan-86	11	317	NO PUP
06-Mar-86	36	353	NO PUP
09-Mar-86	3	356	NO PUP
10-Mar-86	1	357	NO PUP
13-Mar-86	3	360	NO PUP
17-Mar-86	4	364	NO PUP
01-Apr-86	15	379	NO PUP
26-Apr-86	25	404	NO PUP
05-Jul-86	70	474	NO PUP
06-Aug-86	32	506	NO PUP
27-Aug-86	21	527	NO PUP
30-Aug-86	3	530	NO PUP
12-Sep-86	13	543	NO PUP
03-Jan-87	113	656	NO PUP
14-Feb-87	42	698	PUP
16-Mar-87	30	728	PUP

SEA OTTER 15

DATE	DAYS BETWEEN	CUM DAYS	STATUS
21-Mar-85			NO PUP
22-Mar-85	1	1	NO PUP
24-Mar-85	2	3	NO PUP
26-Mar-85	2	5	NO PUP
27-Mar-85	1	6	NO PUP
28-Mar-85	1	7	NO PUP
29-Mar-85	1	8	NO PUP
30-Mar-85	1	9	NO PUP
31-Mar-85	1	10	NO PUP
01-Apr-85	1	11	NO PUP
02-Apr-85	1	12	NO PUP
06-Apr-85	4	16	NO PUP
08-Apr-85	2	18	NO PUP
11-Apr-85	3	21	NO PUP
12-Apr-85	1	22	NO PUP
13-Apr-85	1	23	NO PUP
14-Apr-85	1	24	NO PUP
15-Apr-85	1	25	NO PUP
16-Apr-85	1	26	NO PUP
17-Apr-85	1	27	NO PUP
18-Apr-85	1	28	NO PUP
20-Apr-85	2	30	NO PUP
22-Apr-85	2	32	NO PUP
28-Apr-85	6	38	NO PUP
30-Apr-85	2	40	NO PUP
02-May-85	2	42	NO PUP
03-May-85	1	43	NO PUP
04-May-85	1	44	NO PUP
05-May-85	1	45	NO PUP
06-May-85	1	46	NO PUP
07-May-85	1	47	NO PUP
07-May-85	0	47	NO PUP
11-May-85	4	51	NO PUP
12-May-85	1	52	NO PUP
13-May-85	1	53	NO PUP
15-May-85	2	55	NO PUP
16-May-85	1	56	NO PUP
17-May-85	1	57	NO PUP
23-May-85	6	63	NO PUP
24-May-85	1	64	NO PUP
25-May-85	1	65	NO PUP
26-May-85	1	66	NO PUP
28-May-85	2	68	NO PUP
02-Jun-85	5	73	NO PUP
06-Jun-85	4	77	NO PUP
08-Jun-85	2	79	NO PUP

SEA OTTER 15 (cont.)

DATE	DAYS BETWEEN	CUM DAYS	STATUS
10-Jun-85	2	81	NO PUP
11-Jun-85	1	82	NO PUP
12-Jun-85	1	83	NO PUP
24-Jun-85	12	95	NO PUP
25-Jun-85	1	96	NO PUP
29-Jun-85	4	100	NO PUP
01-Jul-85	2	102	NO PUP
03-Jul-85	2	104	NO PUP
06-Jul-85	3	107	NO PUP
08-Jul-85	2	109	NO PUP
25-Jul-85	17	126	NO PUP
25-Jul-85	0	126	NO PUP
27-Jul-85	2	128	NO PUP
29-Jul-85	2	130	NO PUP
31-Jul-85	2	132	NO PUP
01-Aug-85	1	133	NO PUP
02-Aug-85	1	134	NO PUP
05-Aug-85	3	137	NO PUP
14-Aug-85	9	146	NO PUP
16-Aug-85	2	148	NO PUP
17-Aug-85	1	149	NO PUP
19-Aug-85	2	151	NO PUP
20-Aug-85	1	152	NO PUP
23-Aug-85	3	155	NO PUP
24-Aug-85	1	156	NO PUP
27-Aug-85	3	159	NO PUP
31-Aug-85	4	163	NO PUP
01-Sep-85	1	164	NO PUP
04-Sep-85	3	167	NO PUP
05-Sep-85	1	168	NO PUP
06-Sep-85	1	169	NO PUP
07-Sep-85	1	170	NO PUP
10-Sep-85	3	173	NO PUP
12-Sep-85	2	175	NO PUP
13-Sep-85	1	176	NO PUP
19-Sep-85	6	182	NO PUP
24-Sep-85	5	187	NO PUP
25-Sep-85	1	188	NO PUP
28-Sep-85	3	191	NO PUP
10-Oct-85	12	203	NO PUP
14-Oct-85	4	207	NO PUP
15-Oct-85	1	208	NO PUP
16-Oct-85	1	209	NO PUP
18-Oct-85	2	211	NO PUP
21-Oct-85	3	214	NO PUP
23-Oct-85	2	216	NO PUP
26-Oct-85	3	219	NO PUP

SEA OTTER 15 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
31-Oct-85	5	224	NO PUP
07-Nov-85	7	231	NO PUP
11-Nov-85	4	235	NO PUP
12-Nov-85	1	236	NO PUP
15-Nov-85	3	239	NO PUP
19-Nov-85	4	243	NO PUP
20-Nov-85	1	244	NO PUP
08-Dec-85	18	262	NO PUP
10-Dec-85	2	264	NO PUP
13-Dec-85	3	267	NO PUP
14-Dec-85	1	268	NO PUP
28-Dec-85	14	282	NO PUP
03-Jan-86	6	288	NO PUP
08-Jan-86	5	293	NO PUP
09-Jan-86	1	294	NO PUP
13-Jan-86	4	298	NO PUP
18-Jan-86	5	303	NO PUP
24-Jan-86	6	309	NO PUP
25-Jan-86	1	310	NO PUP
28-Jan-86	3	313	NO PUP
03-Feb-86	6	319	NO PUP
07-Feb-86	4	323	NO PUP
08-Feb-86	1	324	NO PUP
13-Feb-86	5	329	NO PUP
15-Feb-86	2	331	NO PUP
19-Feb-86	4	335	NO PUP
06-Mar-86	15	350	NO PUP
10-Mar-86	4	354	NO PUP
12-Mar-86	2	356	NO PUP
13-Mar-86	1	357	NO PUP
24-Mar-86	11	368	NO PUP
10-Apr-86	17	385	NO PUP
18-Apr-86	8	393	NO PUP
29-Apr-86	11	404	NO PUP
18-May-86	19	423	NO PUP
10-Jun-86	23	446	NO PUP
24-Jun-86	14	460	NO PUP
05-Jul-86	11	471	NO PUP
28-Jul-86	23	494	NO PUP
05-Aug-86	8	502	NO PUP
08-Aug-86	3	505	NO PUP
27-Aug-86	19	524	NO PUP
12-Sep-86	16	540	NO PUP
03-Oct-86	21	561	NO PUP
09-Oct-86	6	567	NO PUP
02-Nov-86	24	591	NO PUP
08-Nov-86	6	597	NO PUP

SEA OTTER 15 (cont.)

DATE	DAYS BETWEEN	CUM DAYS	STATUS
26-Nov-86	18	615	NO PUP
13-Dec-86	17	632	NO PUP
15-Dec-86	2	634	PUP
07-Jan-87	23	657	PUP
06-Mar-87	58	715	PUP

SEA OTTER 16 (cont.)

DATE	DAYS BETWEEN	CUM DAYS	STATUS
08-Apr-85			NO PUP
09-Apr-85	1	1	NO PUP
11-Apr-85	2	3	NO PUP
13-Apr-85	2	5	NO PUP
15-Apr-85	2	7	NO PUP
20-Apr-85	5	12	NO PUP
25-Apr-85	5	17	NO PUP
06-May-85	11	28	NO PUP
16-May-85	10	38	NO PUP
01-Jul-85	46	84	NO PUP
06-Jul-85	5	89	NO PUP
16-Aug-85	41	130	PUP
25-Sep-85	40	170	PUP
15-Nov-85	51	221	PUP
11-Dec-85	26	247	PUP
25-Mar-86	104	351	NO PUP
30-Apr-86	36	387	NO PUP
12-Jun-86	43	430	NO PUP
04-Jul-86	22	452	NO PUP
01-Nov-86	120	572	NO PUP
23-Nov-86	22	594	NO PUP
29-Nov-86	6	600	NO PUP

SEA OTTER 19

DATES	DAYS BETWEEN	CUM DAYS	STATUS
08-Apr-85			
09-Apr-85	1	1	PUP
11-Apr-85	2	3	PUP
11-Apr-85	0	3	PUP
22-Apr-85	11	14	NO PUP
25-Apr-85	3	17	NO PUP
02-May-85	7	24	NO PUP
06-May-85	4	28	NO PUP
16-May-85	10	38	NO PUP
17-Jun-85	32	70	NO PUP
01-Jul-85	14	84	NO PUP
06-Jul-85	5	89	NO PUP
22-Aug-85	47	136	NO PUP
07-Sep-85	16	152	NO PUP
14-Nov-85	68	220	PUP
15-Nov-85	1	221	PUP
19-Nov-85	4	225	PUP
11-Dec-85	22	247	PUP
03-Jan-86	23	270	PUP
07-Feb-86	35	305	PUP
28-Apr-86	80	385	NO PUP
06-Jul-86	69	454	NO PUP
28-Jul-86	22	476	NO PUP
23-Sep-86	57	533	PUP
28-Sep-86	5	538	PUP
27-Oct-86	29	567	PUP
01-Nov-86	5	572	PUP
06-Nov-86	5	577	NO PUP

SEA OTTER 22

DATES	DAYS BETWEEN	CUM DAYS	STATUS
12-Apr-85			NO PUP
20-Apr-85	8	8	NO PUP
09-May-85	19	27	NO PUP
10-May-85	1	28	NO PUP
12-May-85	2	30	NO PUP
13-May-85	1	31	NO PUP
15-May-85	2	33	NO PUP
16-May-85	1	34	NO PUP
24-May-85	8	42	NO PUP
08-Jun-85	15	57	NO PUP
10-Jun-85	2	59	NO PUP
12-Jun-85	2	61	NO PUP
13-Jun-85	1	62	NO PUP
17-Jun-85	4	66	NO PUP
26-Jun-85	9	75	NO PUP
29-Jun-85	3	78	NO PUP
04-Jul-85	5	83	NO PUP
06-Jul-85	2	85	NO PUP
21-Jul-85	15	100	NO PUP
22-Jul-85	1	101	NO PUP
28-Jul-85	6	107	NO PUP
29-Jul-85	1	108	NO PUP
04-Aug-85	6	114	NO PUP
16-Aug-85	12	126	NO PUP
17-Aug-85	1	127	NO PUP
25-Aug-85	8	135	NO PUP
31-Aug-85	6	141	NO PUP
10-Oct-85	40	181	NO PUP
13-Nov-85	34	215	NO PUP
30-Nov-85	17	232	NO PUP
03-Dec-85	3	235	NO PUP
12-Dec-85	9	244	NO PUP
15-Jan-86	34	278	NO PUP
16-Jan-86	1	279	NO PUP
22-Jan-86	6	285	NO PUP
10-Feb-86	19	304	NO PUP
19-Feb-86	9	313	NO PUP
01-Jun-86	102	415	NO PUP
09-Sep-86	100	515	NO PUP
22-Oct-86	43	558	NO PUP
12-Nov-86	21	579	NO PUP

SEA OTTER 25

DATES	DAYS BETWEEN	CUM DAYS	STATUS
20-Apr-85			NO PUP
22-Apr-85	2	2	PUP
23-Apr-85	1	3	PUP
28-Apr-85	5	8	PUP
01-May-85	3	11	PUP
06-May-85	5	16	PUP
07-May-85	1	17	PUP
11-May-85	4	21	PUP
16-May-85	5	26	PUP
17-May-85	1	27	PUP
28-May-85	11	38	PUP
10-Jun-85	13	1	PUP
23-Jun-85	13	64	PUP
25-Jun-85	2	66	PUP
29-Jun-85	4	70	PUP
01-Jul-85	2	72	PUP
02-Jul-85	1	73	PUP
03-Jul-85	1	74	PUP
04-Jul-85	1	75	PUP
0-Jul-85	16	1	PUP
29-Jul-85	9	100	PUP
31-Jul-85	2	102	PUP
01-Aug-85	1	103	PUP
05-Aug-85	4	107	PUP
15-Aug-85	10	117	PUP
16-Aug-85	1	118	PUP
17-Aug-85	1	119	PUP
18-Aug-85	1	120	PUP
19-Aug-85	1	121	PUP
19-Aug-85	0	121	PUP
20-Aug-85	1	122	PUP
21-Aug-85	1	123	PUP
22-Aug-85	1	124	PUP
23-Aug-85	1	125	PUP
24-Aug-85	1	126	PUP
27-Aug-85	3	129	PUP
31-Aug-85	4	133	PUP
01-Sep-85	1	134	PUP
02-Sep-85	1	135	PUP
03-Sep-85	1	136	PUP
04-Sep-85	1	137	PUP
04-Sep-85	0	137	PUP
05-Sep-85	1	138	PUP
06-Sep-85	1	139	PUP
07-Sep-85	1	140	PUP
10-Sep-85	3	143	PUP
12-Sep-85	2	145	PUP
15-Sep-85	3	148	PUP
18-Sep-85	3	151	PUP

SEA OTTER 25 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
24-Sep-85	6	157	PUP
25-Sep-85	1	158	PUP
28-Sep-85	3	161	PUP
30-Sep-85	2	163	PUP
03-Oct-85	3	166	PUP
08-Oct-85	5	171	PUP
10-Oct-85	2	173	PUP
14-Oct-85	4	177	PUP
15-Oct-85	1	178	PUP
23-Oct-85	8	186	NO PUP
29-Oct-85	6	192	NO PUP
30-Oct-85	1	193	NO PUP
31-Oct-85	1	194	NO PUP
01-Nov-85	1	195	NO PUP
07-Nov-85	6	201	NO PUP
11-Nov-85	4	205	NO PUP
12-Nov-85	1	206	NO PUP
15-Nov-85	3	209	NO PUP
20-Nov-85	5	214	NO PUP
29-Nov-85	9	223	NO PUP
04-Dec-85	5	228	NO PUP
08-Dec-85	4	232	NO PUP
14-Dec-85	6	238	NO PUP
15-Dec-85	1	239	NO PUP
27-Dec-85	12	251	NO PUP
03-Jan-86	7	258	NO PUP
08-Jan-86	5	263	NO PUP
13-Jan-86	5	268	NO PUP
15-Jan-86	2	270	NO PUP
18-Jan-86	3	273	NO PUP
19-Jan-86	1	274	NO PUP
23-Jan-86	4	278	NO PUP
04-Feb-86	12	290	NO PUP
08-Feb-86	4	294	NO PUP
11-Feb-86	3	297	NO PUP
13-Feb-86	2	299	NO PUP
15-Feb-86	2	301	NO PUP
19-Feb-86	4	305	NO PUP
01-Mar-86	10	315	NO PUP
06-Mar-86	5	320	NO PUP
10-Mar-86	4	324	NO PUP
12-Mar-86	2	326	NO PUP
13-Mar-86	1	327	NO PUP
17-Mar-86	4	331	NO PUP
24-Mar-86	7	338	NO PUP
25-Mar-86	1	339	NO PUP
10-Apr-86	16	355	NO PUP
28-Apr-86	18	373	NO PUP
29-Apr-86	1	374	NO PUP

SEA OTTER 25 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
31-May-86	32	406	NO PUP
10-Jun-86	10	416	NO PUP
24-Jun-86	14	430	NO PUP
05-Jul-86	11	441	NO PUP
07-Jul-86	2	443	NO PUP
06-Aug-86	30	473	NO PUP
08-Aug-86	2	475	NO PUP
12-Sep-86	35	510	NO PUP
21-Sep-86	9	519	NO PUP
03-Oct-86	12	531	NO PUP
16-Oct-86	13	544	NO PUP

SEA OTTER 27

DATES	DAYS BETWEEN	CUM DAYS	STATUS
04-Oct-85			NO PUP
07-Oct-85	3	3	NO PUP
09-Oct-85	2	5	NO PUP
11-Oct-85	2	7	NO PUP
16-Oct-85	5	12	NO PUP
17-Oct-85	1	13	NO PUP
23-Oct-85	6	19	NO PUP
28-Oct-85	5	24	NO PUP
30-Oct-85	2	26	NO PUP
31-Oct-85	1	27	NO PUP
11-Nov-85	11	38	NO PUP
11-Nov-85	0	38	NO PUP
16-Nov-85	5	43	NO PUP
29-Nov-85	13	56	NO PUP
10-Dec-85	11	67	NO PUP
14-Dec-85	4	71	NO PUP
15-Dec-85	1	72	NO PUP
20-Dec-85	5	77	NO PUP
27-Dec-85	7	84	NO PUP
28-Dec-85	1	85	NO PUP
30-Dec-85	2	87	NO PUP
03-Jan-86	4	91	NO PUP
08-Jan-86	5	96	NO PUP
09-Jan-86	1	97	NO PUP
15-Jan-86	6	103	NO PUP
18-Jan-86	3	106	NO PUP
22-Jan-86	4	110	NO PUP
23-Jan-86	1	111	NO PUP
28-Jan-86	5	116	NO PUP
08-Feb-86	11	127	NO PUP
11-Feb-86	3	130	NO PUP
13-Feb-86	2	132	NO PUP
06-Mar-86	21	153	NO PUP
10-Mar-86	4	157	NO PUP
12-Mar-86	2	159	NO PUP
24-Mar-86	12	171	NO PUP
02-Apr-86	9	180	NO PUP
18-Apr-86	16	196	NO PUP
29-Apr-86	11	207	PUP
05-May-86	6	213	PUP
23-May-86	18	231	PUP
18-Jun-86	26	257	NO PUP
24-Jun-86	6	263	NO PUP
05-Jul-86	11	274	NO PUP
28-Jul-86	23	297	NO PUP
29-Aug-86	32	329	NO PUP
17-Sep-86	19	348	NO PUP
27-Sep-86	10	358	NO PUP
28-Sep-86	1	359	NO PUP

SEA OTTER 27 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
04-Nov-86	37	396	NO PUP
07-Nov-86	3	399	NO PUP
12-Nov-86	5	404	NO PUP
28-Mar-87	136	540	NO PUP

SEA OTTER 31

DATES	DAYS BETWEEN	CUM DAYS	STATUS
16-Oct-85			NO PUP
21-Oct-85	5	5	NO PUP
23-Oct-85	2	7	NO PUP
28-Oct-85	5	12	NO PUP
30-Oct-85	2	14	NO PUP
07-Nov-85	8	22	NO PUP
15-Nov-85	8	30	NO PUP
16-Nov-85	1	31	NO PUP
10-Dec-85	24	55	NO PUP
12-Dec-85	2	57	NO PUP
20-Dec-85	8	65	NO PUP
28-Dec-85	8	73	NO PUP
03-Jan-86	6	79	NO PUP
21-Jan-86	18	97	NO PUP
23-Jan-86	2	99	NO PUP
24-Jan-86	1	100	NO PUP
28-Jan-86	4	104	NO PUP
05-Feb-86	8	112	PUP
08-Feb-86	3	115	PUP
10-Feb-86	2	117	PUP
13-Feb-86	3	120	PUP
15-Feb-86	2	122	PUP
19-Feb-86	4	126	PUP
21-Feb-86	2	128	PUP
01-Mar-86	8	136	NO PUP
05-Mar-86	4	140	NO PUP
06-Mar-86	1	141	NO PUP
10-Mar-86	4	145	NO PUP
12-Mar-86	2	147	NO PUP
27-Mar-86	15	162	NO PUP
01-Apr-86	5	167	NO PUP
06-Apr-86	5	172	NO PUP
10-Apr-86	4	176	NO PUP
18-Apr-86	8	184	NO PUP
24-Apr-86	6	190	NO PUP
29-Jun-86	66	256	NO PUP
08-Aug-86	40	296	NO PUP
29-Aug-86	21	317	NO PUP
12-Sep-86	14	331	NO PUP
09-Oct-86	27	358	NO PUP
23-Oct-86	14	372	NO PUP
08-Jan-87	77	449	NO PUP
05-Feb-87	28	477	PUP
02-Mar-87	25	502	PUP
16-Mar-87	14	516	NO PUP
18-Mar-87	2	518	NO PUP
07-Apr-87	20	538	NO PUP
28-Apr-87	21	559	NO PUP

SEA OTTER 33

DATES	DAYS BETWEEN	CUM DAYS	STATUS
03-Jul-84			
23-Oct-85			NO PUP
29-Oct-85	6		NO PUP
30-Oct-85	1	7	NO PUP
31-Oct-85	1	8	NO PUP
02-Nov-85	2	10	NO PUP
07-Nov-85	5	15	NO PUP
12-Nov-85	5	20	NO PUP
14-Nov-85	2	22	NO PUP
17-Nov-85	3	25	NO PUP
19-Nov-85	2	27	NO PUP
20-Nov-85	1	28	NO PUP
29-Nov-85	9	37	NO PUP
08-Dec-85	9	46	NO PUP
12-Dec-85	4	50	NO PUP
14-Dec-85	2	52	NO PUP
03-Jan-86	20	72	NO PUP
10-Jan-86	7	79	NO PUP
13-Jan-86	3	82	NO PUP
22-Jan-86	9	91	NO PUP
23-Jan-86	1	92	NO PUP
24-Jan-86	1	93	NO PUP
25-Jan-86	1	94	NO PUP
28-Jan-86	3	97	NO PUP
07-Feb-86	10	107	PUP
09-Feb-86	2	109	PUP
11-Feb-86	2	111	PUP
13-Feb-86	2	113	PUP
15-Feb-86	2	115	PUP
19-Feb-86	4	119	PUP
23-Feb-86	4	123	PUP
24-Feb-86	1	124	PUP
01-Mar-86	5	129	PUP
08-Mar-86	7	136	PUP
10-Mar-86	2	138	PUP
12-Mar-86	2	140	NO PUP
13-Mar-86	1	141	NO PUP
25-Mar-86	12	153	NO PUP
24-Apr-86	30	183	NO PUP
10-Jun-86	47	230	NO PUP
24-Jun-86	14	244	NO PUP
06-Aug-86	43	287	NO PUP
08-Aug-86	2	289	NO PUP
29-Aug-86	21	310	NO PUP
03-Oct-86	35	345	NO PUP
01-Nov-86	29	374	NO PUP
17-Dec-86	46	420	NO PUP
23-Mar-87	96	516	NO PUP
28-Mar-87	5	521	PUP

SEA OTTER 33 (cont.)

DATES	DAYS BETWEEN	CUM DAYS	STATUS
05-Apr-87	8	529	PUP
24-Apr-87	19	548	NO PUP

SEA OTTER 36

DATES	DAYS BETWEEN	CUM DAYS	STATUS
18-Nov-85			NO PUP
19-Nov-85	1	1	NO PUP
22-Nov-85	3	4	NO PUP
25-Nov-85	3	7	NO PUP
06-Dec-85	11	18	NO PUP
09-Dec-85	3	21	NO PUP
20-Dec-85	11	32	NO PUP
15-Jan-86	26	58	NO PUP
21-Jan-86	6	64	NO PUP
05-Feb-86	15	79	NO PUP
11-Feb-86	6	85	NO PUP
27-Feb-86	16	101	NO PUP
08-Apr-86	40	141	NO PUP
14-Apr-86	6	147	NO PUP
21-May-86	37	184	PUP
22-May-86	1	185	PUP
06-Jun-86	15	200	PUP
11-Jun-86	5	205	PUP
13-Jun-86	2	207	PUP
16-Jun-86	3	210	PUP DEAD
18-Jun-86	2	212	PUP GONE
19-Jun-86	1	213	NO PUP
16-Jul-86	27	240	NO PUP
17-Jul-86	1	241	NO PUP
22-Jul-86	5	246	NO PUP
01-Aug-86	10	256	NO PUP
08-Aug-86	7	263	NO PUP
15-Aug-86	7	270	NO PUP
29-Aug-86	14	284	NO PUP
04-Sep-86	6	290	NO PUP
10-Sep-86	6	296	NO PUP
12-Sep-86	2	298	NO PUP
03-Oct-86	21	319	NO PUP
07-Oct-86	4	323	NO PUP
10-Nov-86	34	357	NO PUP
16-Nov-86	6	363	NO PUP
18-Nov-86	2	365	NO PUP
25-Nov-86	7	372	NO PUP
30-Nov-86	5	377	NO PUP
12-Dec-86	12	389	NO PUP
17-Dec-86	5	394	NO PUP
24-Dec-86	7	401	NO PUP
03-Mar-87	69	470	NO PUP
20-Mar-87	17	487	PUP
25-Mar-87	5	492	NO PUP

Appendix 2.2 Data on instrumented otters used for estimating survival rates.

OTTER NUMBER	SEX	CAPTURE DATE	LAST DATE TX HEARD	STATUS	DAYS TRANSMITTING	LAST DATE RECOGNIZED BY TAGS
1	AM	07-MAR-84	28-MAY-85	MISSING	447	
2	AM	16-MAR-84	15-SEP-84	MISSING	183	
3	AM	21-MAR-84	28-AUG-85	TX EXPIRED	525	
4	AM	21-MAR-84	28-AUG-85	TX EXPIRED	523	26-Nov-86
6	AF	03-JUL-84	23-JUN-85	TX EXPIRED	355	
7	AM	15-FEB-85	10-NOV-86	MISSING	633	
9	AF	01-MAR-85	27-AUG-86	MISSING	544	
10	AM	01-MAR-85	12-NOV-86	MISSING	621	
11	AF	15-MAR-85	26-NOV-86	MISSING	621	
13	JM	16-MAR-85	05-JAN-87	MISSING	660	11-Aug-87
14	AF	16-MAR-85	30-MAR-87	MISSING	744	
15	AF	20-MAR-85	11-DEC-86	TX EXPIRED	631	06-Mar-87
16	AF	03-APR-85	02-DEC-86	MISSING	608	
17	AM	03-APR-85	28-MAR-86	MISSING	359	
19	AF	03-APR-85	11-NOV-86	MISSING	587	
21	AF	10-APR-85	13-APR-85	MISSING	3	
22	AF	10-APR-85	16-NOV-86	MISSING	585	
23	AM	10-APR-85	27-APR-85	DEAD	17	
25	AF	13-APR-85	20-OCT-86	MISSING	555	
26	AF	08-MAY-85	05-JUN-85	DEAD	28	
27	AF	04-OCT-85	31-OCT-86	TX EXPIRED	392	28-Mar-87
28	AF	04-OCT-85	04-NOV-85	TX FAILED	31	
29	JF	11-OCT-85	14-MAR-87	MISSING	519	
30	JM	11-OCT-85	29-JUL-87	MISSING	656	
31	AF	11-OCT-85	24-JUL-87	MISSING	651	
33	AF	18-OCT-85	26-SEP-87	MISSING	708	
34	AM	19-OCT-85	23-SEP-86	MISSING	339	
35	JM	08-NOV-85	21-MAR-87	MISSING	498	
36	AF	08-NOV-85	07-OCT-87	MISSING	698	
37	JF	22-NOV-85	17-OCT-86	MISSING	329	
38	JF	22-NOV-85	02-JAN-86	MISSING	41	
39	JF	22-NOV-85	25-MAR-87	MISSING	488	
40	JF	17-DEC-85	03-DEC-87	TRANSMITTING	716	
41	JM	17-DEC-85	13-APR-87	DEAD	482	
42	JF	17-DEC-85	09-OCT-87	MISSING	661	
43	JM	18-DEC-85	10-NOV-87	MISSING	692	
44	JF	18-DEC-85	29-JUN-86	DEAD	193	
45	JF	18-DEC-85	22-MAR-87	MISSING	459	
46	JF	18-DEC-85	25-DEC-87	TRANSMITTING	737	
47	JF	30-DEC-85	28-DEC-87	TRANSMITTING	728	

Appendix 2.3 -- Tag loss information for instrumented sea otters in California as of
10 July 1987.

OTTER NUMBER	DATE TAGGED	RIGHT TAG LAST SEEN	RIGHT TAG MISSING	LEFT TAG LAST SEEN	LEFT TAG MISSING	DAYS FROM TAGGING TO DATE LAST SEEN OR MISSING RIGHT TAG	DAYS FROM TAGGING TO DATE LAST SEEN OR MISSING LEFT TAG
1	07-MAR-84	28-MAY-85		28-MAY-85		447	447
2	16-MAR-84	15-SEP-84		15-SEP-85		183	183
3	21-MAR-84	28-AUG-85		28-AUG-85		525	525
4	21-MAR-84	26-NOV-86		26-NOV-86		980	980
6	03-JUL-84	21-FEB-85	06-MAR-85	21-JUN-85		246	353
7	15-FEB-85	06-AUG-86		06-AUG-85		537	537
9	01-MAR-85	07-OCT-85	23-OCT-85	05-FEB-86	29-APR-86	236	424
10	01-MAR-85	14-NOV-85	06-APR-86	11-SEP-85	14-NOV-85	401	258
11	15-MAR-85	07-SEP-85		07-SEP-85		176	176
13	16-MAR-85	31-AUG-85		31-AUG-85		168	168
14	16-MAR-85	25-SEP-85	15-NOV-85	29-JUN-85	24-JUL-85	244	130
15	20-MAR-85	06-MAR-87		06-MAR-87		716	716
16	03-APR-85	16-AUG-85	11-SEP-85	16-AUG-85	11-SEP-85	161	161
17	03-APR-85	11-NOV-85		11-NOV-85		222	222
19	03-APR-85	01-NOV-86		11-SEP-85	11-DEC-85	577	252
21	10-APR-85	13-APR-85		13-APR-85		3	3
22	10-APR-85	22-OCT-86		22-OCT-85		560	560
23	10-APR-85	27-APR-85		27-APR-85		17	17
25	13-APR-85	21-SEP-86	03-OCT-86	24-JUN-86	06-AUG-86	538	480
26	08-MAY-85	06-JUN-85		06-JUN-85		29	29
27	04-OCT-85	28-MAR-87		28-MAR-87		540	540
28	04-OCT-85	15-OCT-85		15-OCT-85		11	11
29	11-OCT-85	30-OCT-85	11-FEB-86	30-OCT-85	11-FEB-86	123	123
30	11-OCT-85	30-MAY-87		30-MAY-85		596	596
31	11-OCT-85	18-APR-86	02-MAY-86	16-MAY-87		203	582
33	18-OCT-85	07-JUL-87		07-JUL-87		627	627
34	19-OCT-85	13-AUG-86		06-JUL-86	13-AUG-86	298	298
35	08-NOV-85	03-MAR-87		03-MAR-87		480	480
36	08-NOV-85	01-JUL-87		06-JUL-87		600	605
37	22-NOV-85	17-JUL-86		17-JUL-86		237	237
38	22-NOV-85	18-DEC-85		18-DEC-85		26	26
39	22-NOV-85	28-MAR-87		28-MAR-87		491	491
40	17-DEC-85	06-JUN-86	17-JUL-86	09-JUL-87		212	569
41	17-DEC-85	17-OCT-86		17-OCT-86		304	304
42	17-DEC-85	25-JUN-86	17-JUL-86	25-JUN-86	17-JUL-86	212	212
43	18-DEC-85	28-JAN-86	27-FEB-87	11-APR-87		41	479
44	18-DEC-85	04-JUL-86		04-JUL-86		198	198
45	18-DEC-85	11-JUN-86	17-JUL-86	17-JAN-87		211	395
46	18-DEC-85	09-NOV-86	29-MAR-87	09-NOV-86	29-MAR-87	466	466
47	30-DEC-85	01-JUL-87		01-JUL-87		548	548

APPENDIX 3.1 -- Analysis of variance for the distance between successive locations of individual instrumented sea otters. Log transformed data, base 2.

A. LOCATIONS 18-36 HOURS APART

	df	MS	F	p
Adult females				
Among individuals	12	20.1	37.4	<0.001
Error	3450	0.537		
Juvenile females				
Among individuals	9	8.8	15.8	<0.001
Error	1918	0.557		
Adult males				
Among individuals	7	1.6	4.0	<0.001
Error	1401	0.398		
Juvenile males				
Among individuals	4	5.0	6.8	<0.001
Error	964	0.735		
Age/sex classes				
Among classes	3	185.6	342.2	<0.001
Error	7733	0.542		

B. LOCATIONS MORE THAN 36 HOURS APART

	df	MS	F	p
Adult females				
Among individuals	12	15.8	18.9	<0.001
Error	1441	0.837		
Juvenile females				
Among individuals	9	8.1	7.6	<0.001
Error	913	1.1		
Adult males				
Among individuals	7	33.4	22.1	<0.001
Error	635	1.5		
Juvenile males				
Among individuals	4	1.6	1.0	ns
Error	544	1.6		
Age/sex classes				
Among classes	3	131.7	94.1	<0.001
Error	3533	1.4		

APPENDIX 3.2 -- Analysis of variance for the minimum convex polygon daily home ranges. Log transformed data, base 2.

	df	MS	F	p
Adult females				
Among individuals	4	8.31	5.91	ns
Error	4	1.41		
Juvenile females				
Among individuals	5	3.04	2.77	ns
Error	5	1.10		
Adult males	sample size too small for testing			
Juvenile males				
Among individuals	3	1.90	0.39	ns
Error	7	3.41	4.87	
Age/sex classes after otters				
Among classes	2	25.95	28.51	<0.001
Error		16	0.91	

APPENDIX 3.3 -- Analysis of variance for seasonal differences in monthly harmonic mean home range size. Log transformed data, base 2.

	df	MS	F	p
Adult females				
Among individuals	12	17.08	7.98	<0.001
Season	1	0.40	0.19	ns
Individualxseason	12	0.94	0.44	ns
Error	227	2.14		
Juvenile females				
Among individuals	8	2.36	1.78	ns
Season	1	1.50	1.13	ns
Individualxseason	8	0.98	0.73	ns
Error	137	1.33		
Adult males				
Among individuals	7	9.11	6.70	<0.001
Season	1	0.10	0.07	ns
Individualxseason	7	1.21	0.89	ns
Error	96	1.36		
Juvenile males				
Among individuals	4	5.88	2.47	ns
Season	1	5.80	2.43	ns
Individualxseason	4	1.60	0.67	ns
Error	79	2.38		

APPENDIX 3.4 -- Analysis of variance for differences in monthly harmonic mean home range size among age/sex classes. Log transformed data, base 2.

	df	MS	F	p
Adult females				
Among individuals	12	17.08	8.29	<0.001
Error	240	2.06		
Juvenile females				
Among individuals	8	2.45	1.87	ns
Error	145	0.557		
Adult males				
Among individuals	7	8.47	5.92	<0.001
Error	105	1.43		
Juvenile males				
Among individuals	4	5.89	2.47	ns
Error	84	2.38		
Age/sex classes after otters				
Among classes	3	294.87	163.8	<0.001
Error	574	1.80		

*This test does not include seasonal effects. The only age/sex group with significant seasonal effects was the juvenile females (see appendix 3.4). Variation due to season is included in the error term; thus, this test is conservative.

APPENDIX 3.5 - Analysis of variance for the distance between extreme locations of individual instrumented sea otters. Log transformed data, base 2.

	df	MS	F	p
Adult females				
Among individuals	12	19.8	22.56	<.001
Error	240	0.88		
Juvenile females				
Among individuals	8	9.81	4.54	<.001
Error	146	2.16		
Adult males				
Among individuals	7	10.13	3.58	< .01
Error	104	2.83		
Juvenile males				
Among individuals	4	2.67	1.68	ns
Error	84	1.59		
Age/Sex classes				
Among classes	3	90.63	54.6	<.001
Error	574	1.66		

APPENDIX 4.1 - TWENTY-FOUR-HOUR DATA BY OBSERVATION PERIOD.

OTTER NUMBER	AGE/ SEX	DATE	LENGTH (HRS)	NUMBER OF 10-MIN PERIODS REST	FEED	OTHER
6	AF	19-Jul-84	24	81	27	38
6	AF	25-Jul-84	48	145	101	62
6	AF	07-Aug-84	24	64	66	20
6	AF	21-Aug-84	14	39	32	14
6	AF	31-Aug-84	24	60	58	33
6	AF	05-Sep-84	17	35	57	15
7	AM	05-Sep-85	24	64	71	12
7	AM	08-Oct-85	24	105	20	20
7	AM	06-Aug-86	24	77	53	13
9	AFP	23-Jul-85	24	49	69	27
9	AF	26-Aug-85	30	73	85	22
10	AM	10-Sep-85	23	37	75	17
11	AF	05-Sep-85	24	64	58	23
11	AF	08-Oct-85	24	61	54	28
13	JM	24-Aug-86	24	65	45	38
14	AFP	24-Jul-85	24	32	86	25
14	AFP	27-Aug-85	18	51	44	12
15	AF	20-May-85	24	79	52	15
15	AF	30-May-85	23	68	61	6
15	AF	03-Jun-85	24	75	45	25
15	AF	18-Jul-85	24	75	45	26
15	AF	12-Aug-85	72	229	128	76
16	AF	19-May-85	24	66	52	26
16	AF	28-May-85	48	147	98	44
16	AF	10-Jul-85	24	75	32	37
16	AF	10-Sep-85	23	66	54	15
16	AF	08-Oct-85	24	75	45	18
16	AFP	04-Nov-86	48	137	104	46
17	AM	02-Jul-85	48	120	105	67
17	AM	19-Jul-85	24	69	69	7
19	AF	19-May-85	23	54	59	24
19	AF	28-May-85	47	130	117	36
19	AF	04-Nov-86	48	173	71	46
19	AF	10-Sep-85	23	62	65	7
19	AF	08-Oct-85	24	94	44	8
22	AF	30-Jul-85	48	166	103	20
22	AF	05-Sep-85	24	77	39	29
22	AF	08-Oct-85	24	71	49	20
25	AFP	07-Aug-85	48	159	152	45
25	AFP	28-Aug-85	11	35	16	15
27	AFP	13-May-85	48	138	97	54
29	JF	25-Jun-86	24	40	69	36
30	JM	23-Apr-86	48	113	98	80
34	AM	30-Jul-86	24	88	24	32
34	AM	13-Aug-86	24	70	60	15
35	JM	25-Feb-86	50	87	116	89
35	JM	16-Sep-86	48	66	109	114
36	AF	13-Mar-86	24	43	85	17

APPENDIX 4.1 (cont.)

OTTER NUMBER	AGE/ SEX	DATE	LENGTH (HRS)	NUMBER OF 10-MIN PERIODS REST	FEED	OTHER
36	AFP	21-May-86	48	172	86	33
37	JF	06-Mar-86	24	55	85	6
39	JF	25-Feb-86	33	69	75	53
39	JF	29-Apr-86	24	48	84	14
40	JF	03-Apr-86	48	103	157	29
40	JF	20-Aug-86	24	90	35	20
41	JM	13-Mar-86	24	40	81	23
41	JM	20-Aug-86	24	70	45	29
41	JM	24-Sep-86	48	73	102	115
42	JF	16-Apr-86	49	128	134	30
43	JM	20-Aug-86	24	50	44	50
44	JF	19-Mar-86	48	124	136	30
45	JF	13-Nov-86	48	87	173	27
46	JF	06-Mar-86	21	76	35	12
46	JF	30-Apr-86	24	61	77	6
47	JF	19-Nov-86	48	74	173	47

APPENDIX 4.2 DAYLIGHT DATA BY OBSERVATION PERIOD.

OTTER NUMBER	AGE/SEX	DATE	NUMBER OF 10-MIN PERIODS REST	FEED	OTHER
6	AF	19-Jul-84	58	12	23
6	AF	25-Jul-84	98	58	44
6	AF	07-Aug-84	43	42	10
6	AF	21-Aug-84	22	16	2
6	AF	31-Aug-84	41	22	27
6	AF	05-Sep-84	33	20	5
7	AM	05-Sep-85	19	58	7
7	AM	08-Oct-85	58	12	7
7	AM	06-Aug-86	50	31	8
9	AFP	23-Jul-85	14	69	10
9	AF	26-Aug-85	30	77	14
10	AM	10-Sep-85	13	45	13
11	AF	05-Sep-85	25	42	13
11	AF	08-Oct-85	35	33	9
13	JM	24-Aug-86	32	35	22
14	AFP	24-Jul-85	28	46	20
14	AFP	27-Aug-85	31	21	3
15	AF	20-May-85	38	51	5
15	AF	30-May-85	45	44	3
15	AF	03-Jun-85	50	27	17
15	AF	18-Jul-85	62	14	17
15	AF	12-Aug-85	138	82	45
16	AF	19-May-85	43	36	13
16	AF	28-May-85	101	69	17
16	AF	10-Jul-85	45	25	26
16	AF	10-Sep-85	22	43	8
16	AF	08-Oct-85	28	34	8
16	AFP	04-Nov-86	62	68	11
17	AM	02-Jul-85	77	65	36
17	AM	19-Jul-85	53	38	1
19	AF	19-May-85	36	33	16
19	AF	28-May-85	98	61	20
19	AF	04-Nov-86	76	47	21
19	AF	10-Sep-85	21	49	3
19	AF	08-Oct-85	51	20	6
22	AF	30-Jul-85	103	53	16
22	AF	05-Sep-85	45	18	20
22	AF	08-Oct-85	41	17	14
25	AFP	07-Aug-85	108	95	30
25	AFP	28-Aug-85	30	10	12
27	AFP	13-May-85	111	39	31
29	JF	25-Jun-86	21	42	31
30	JM	23-Apr-86	71	46	58
34	AM	30-Jul-86	43	19	29
34	AM	13-Aug-86	31	48	10
35	JM	25-Feb-86	44	51	61
35	JM	16-Sep-86	22	59	83

APPENDIX 4.2 (cont.)

OTTER NUMBER	AGE/SEX	DATE	NUMBER OF 10-MIN PERIODS REST	FEED	OTHER
36	AF	13-Mar-86	20	48	10
36	AFP	21-May-86	121	43	21
37	JF	06-Mar-86	13	61	4
39	JF	25-Feb-86	46	50	48
39	JF	29-Apr-86	44	38	7
40	JF	03-Apr-86	39	113	13
40	JF	20-Aug-86	61	15	14
41	JM	13-Mar-86	4	53	20
41	JM	20-Aug-86	42	24	21
41	JM	24-Sep-86	34	71	54
42	JF	16-Apr-86	88	53	18
43	JM	20-Aug-86	30	19	38
44	JF	19-Mar-86	37	111	15
45	JF	13-Nov-86	3	124	11
46	JF	06-Mar-86	41	14	3
46	JF	30-Apr-86	38	43	6
47	JF	19-Nov-86	16	96	27

APPENDIX 4.3 VISUAL DATA BY OBSERVATION PERIOD.

OTTER NUMBER	AGE/SEX	DATE	NUMBER OF 10-MIN PERIODS REST	FEED	OTHER
17	AM	02-Jul-85	41	39	24
17	AM	19-Jul-85	43	17	0
10	AM	10-Sep-85	7	0	7
15	AF	18-Jul-85	21	10	6
16	AF	10-Sep-85	5	5	3
9	AF	26-Aug-85	1	5	1
19	AF	10-Sep-85	10	0	1
22	AF	30-Jul-85	90	30	16
15	AF	12-Aug-85	110	32	26
14	AF	24-Jul-85	10	38	17
27	AF	13-May-85	78	21	33
36	AF	21-May-86	115	2	17
25	AF	07-Aug-85	71	28	12
16	AF	19-May-85	10	2	6
16	AF	28-May-85	56	28	10
19	AF	19-May-85	0	0	2
19	AF	28-May-85	22	6	2
15	AF	20-May-85	34	18	4
15	AF	30-May-85	38	23	4
15	AF	03-Jun-85	41	14	15
19	AF	04-Nov-86	11	0	0
7	AM	06-Aug-86	12	9	0
34	AM	13-Aug-86	0	16	0
16	AFP	04-Nov-86	8	17	6
14	AFP	27-Aug-85	11	0	0
29	JF	25-Jun-85	4	11	2
40	JF	20-Aug-86	2	0	0
45	JF	13-Nov-86	0	30	2
47	JF	19-Nov-86	2	8	0
46	JF	06-Mar-86	0	1	0
44	JF	19-Mar-86	17	42	5
46	JF	30-Apr-86	35	42	1
39	JF	29-Apr-86	33	7	1
37	JF	06-Mar-86	3	27	0
40	JF	30-Apr-86	22	64	5
42	JF	16-Apr-86	63	0	4
35	JM	16-Sep-86	0	2	4
35	JM	25-Feb-86	0	6	7
30	JM	23-Apr-86	43	1	17
6	AF	19-Jul-84	37	5	9
6	AF	25-Jul-84	77	35	27
6	AF	07-Aug-84	11	25	1
6	AF	21-Aug-84	10	14	2
6	AF	31-Aug-84	14	17	8
6	AF	05-Sep-84	8	7	1

APPENDIX 5.1 -- Analysis of variance for the length of dives made by individual instrumented sea otters in California. Log-transformed data, base 2.

	df	mean square	F	p
Adult females				
Among individuals	4	130.0	281.4	<0.001
Error	2763	0.46		
Adult females with pups				
Among individuals	3	94.84	144.33	<0.001
Error	1171	0.66		
Juvenile females				
Among individuals	6	76.92	180.52	<0.001
Error	2129	0.43		
Adult males				
Among individuals	6	10.85	14.36	<0.001
Error	1377	0.76		
Juvenile males				
Among individuals	4	7.39	20.04	<0.001
Error	493	0.37		

APPENDIX 5.2 -- Analysis of variance for the length of the surface intervals made by individual instrumented otters. Log-transformed data, base 2.

	df	Mean square	F	p
Adult females				
Among individuals	4	201.3	179.96	<0.001
Error	2656	1.12		
Adult females with pups				
Among individuals	3	31.23	25.42	<0.001
Error	1089	1.23		
Juvenile females				
Among individuals	6	60.75	42.76	<0.001
Error	2114	1.42		
Adult males				
Among individuals	6	28.85	18.37	<0.001
Error	1310	1.57		
Juvenile males				
Among individuals	4	1.38	1.45	ns
Error	472	0.95		

APPENDIX 5.3 - Analysis of variance for the length of dives made during the day and night by the individual instrumented otters.

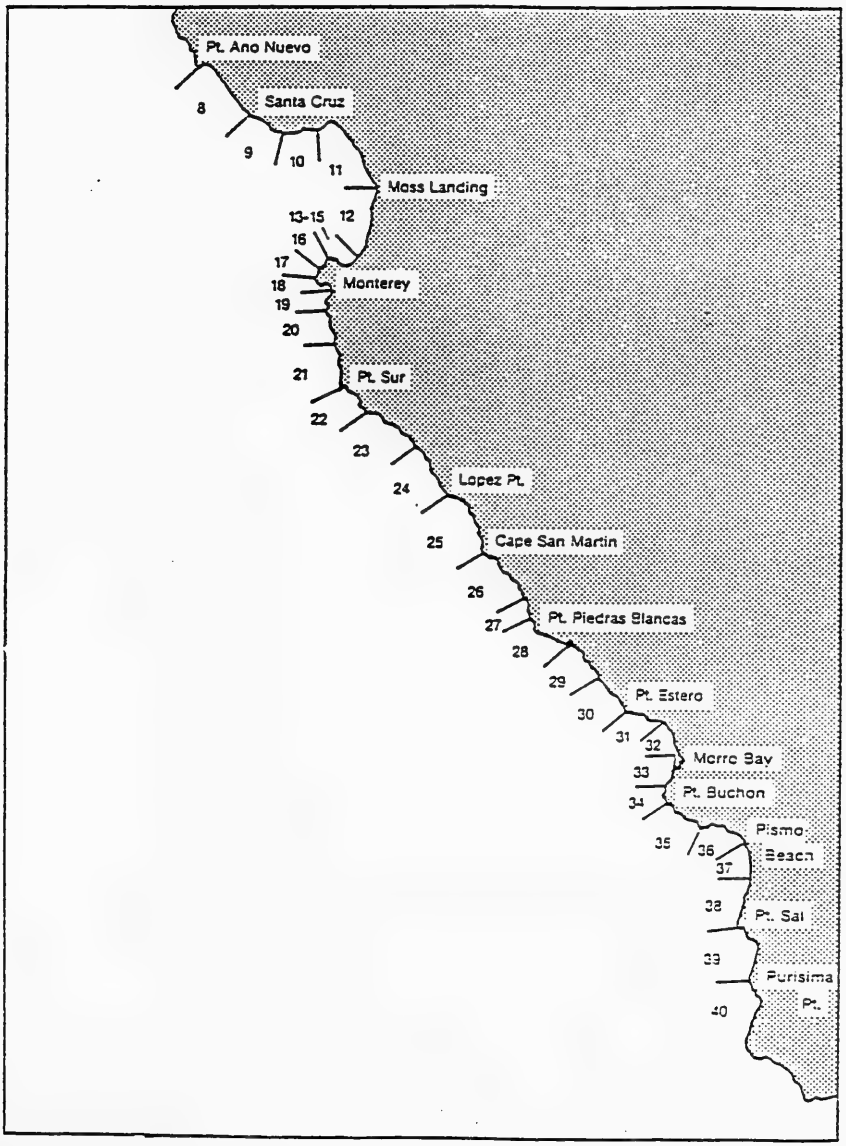
	df	mean square	F	p
Adult females				
Among individuals	4	129.98	302.26	<0.001
Day/night	1	0.10	0.23	ns
Day/night x individual	4	19.55	45.46	<0.001
Error	2758	0.43		
Adult females with pups				
Among individuals	3	94.80	166.37	<0.001
Day/night	1	43.90	77.01	<0.001
Day/night x individual	3	20.30	35.61	<0.001
Error	1167	0.57		
Juvenile males				
Among individuals	4	7.40	21.76	<0.001
Day/night	1	0.90	2.65	ns
Day/night x individual	4	4.48	13.16	<0.001
Error	488	0.34		
Juvenile females				
Among individuals	6	76.92	187.60	<0.001
Day/night	1	8.20	20.00	<0.001
Day/night x individual	6	4.50	10.98	<0.001
Error	2122	0.41		

APPENDIX 5.4 - Analysis of variance for the length of surface intervals made during the day and night by the individual instrumented otters.

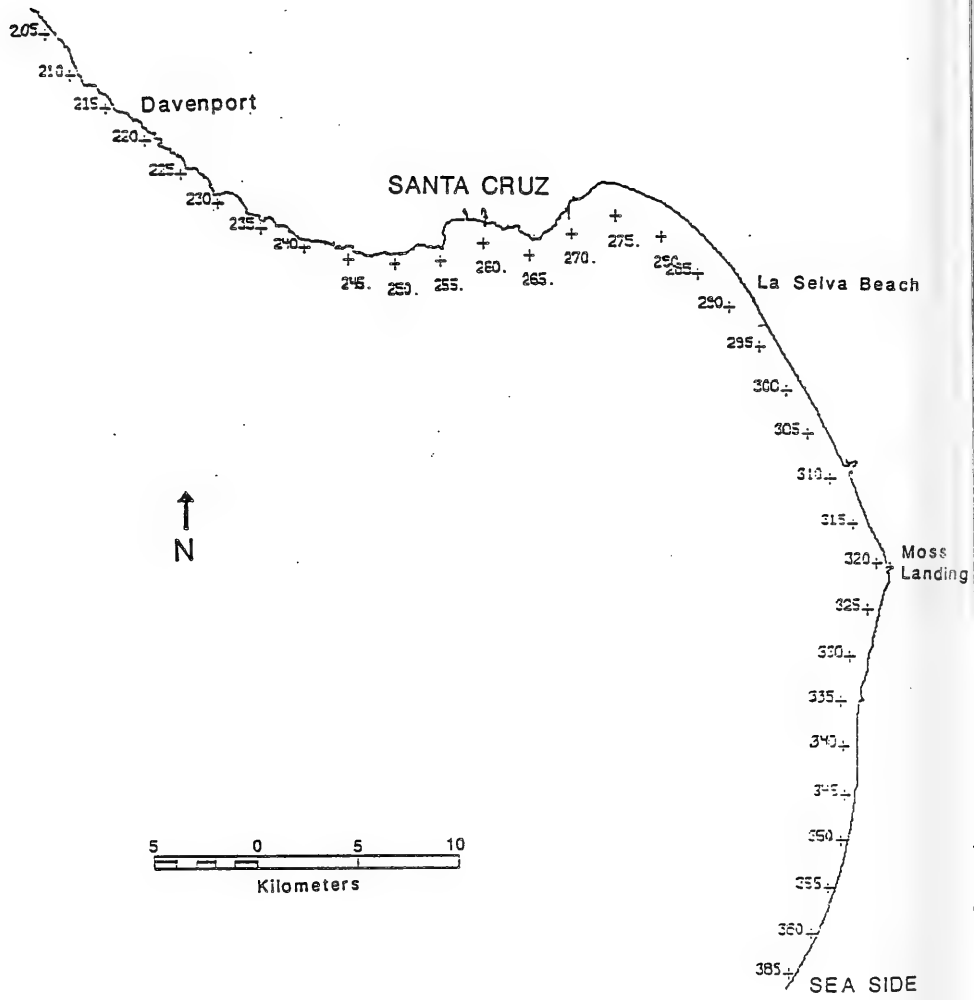
	df	mean square	F	p
Adult females				
Among individuals	4	201.33	181.38	<0.001
Day/night	1	1.11	1.71	ns
Day/night x individual	4	5.52	4.97	<0.01
Error	2651	1.11		
Adult females with pups				
Among individuals	3	31.23	25.39	<0.001
Day/night	1	1.30	1.06	ns
Day/night x individual	3	1.67	1.35	ns
Error	1085	1.23		
Juvenile males				
Among individuals	4	1.38	1.60	ns
Day/night	1	10.80	12.56	<0.001
Day/night x individual	4	9.32	10.84	<0.001
Error	467	0.86		
Juvenile females				
Among individuals	6	60.75	43.70	<0.001
Day/night	1	24.20	17.41	<0.001
Day/night x individual	6	8.55	6.15	<0.001
Error	2107	1.39		

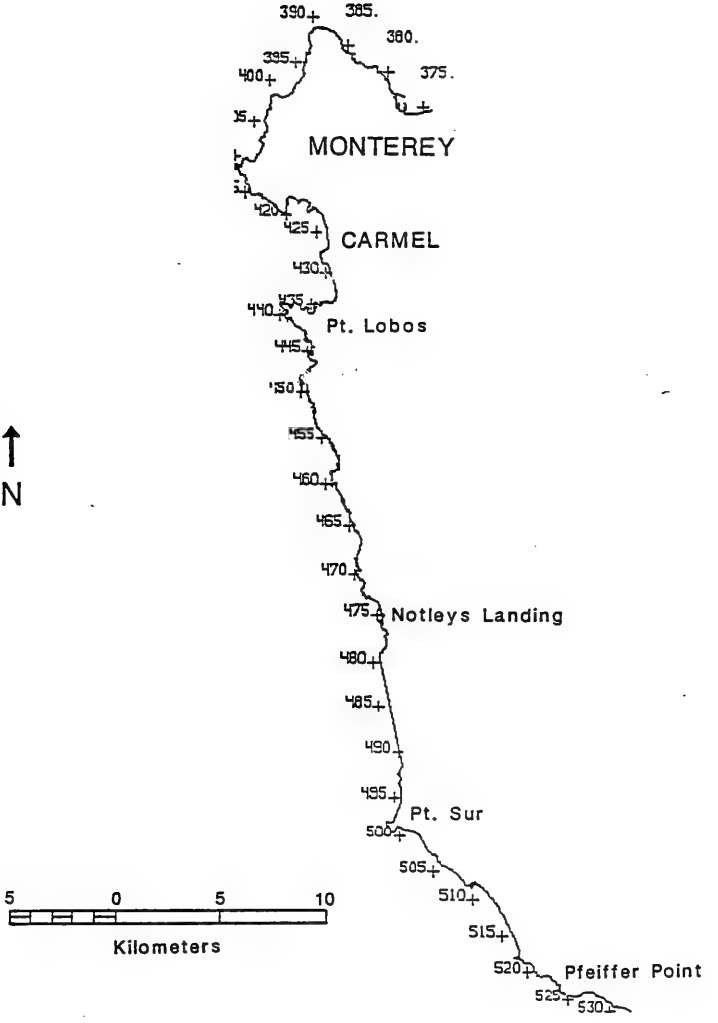
APPENDIX 10.

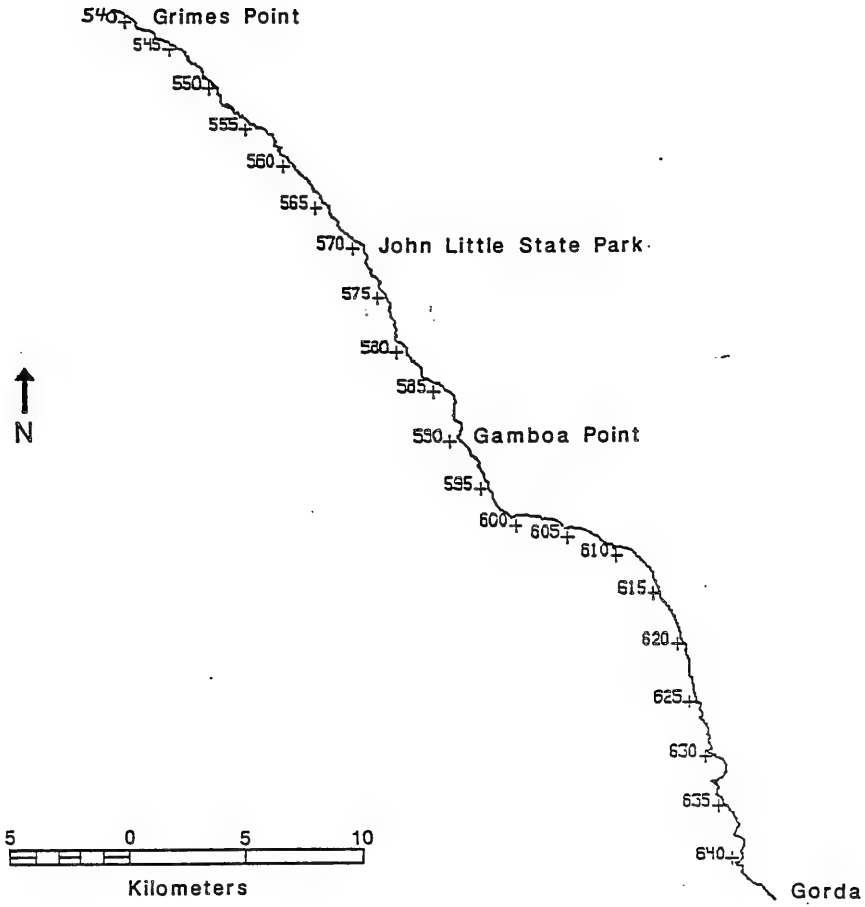
APPENDIX 10.1A -- Map of central California showing California Department of Fish and Game mortality recovery areas (after Ames, et al., 1983).

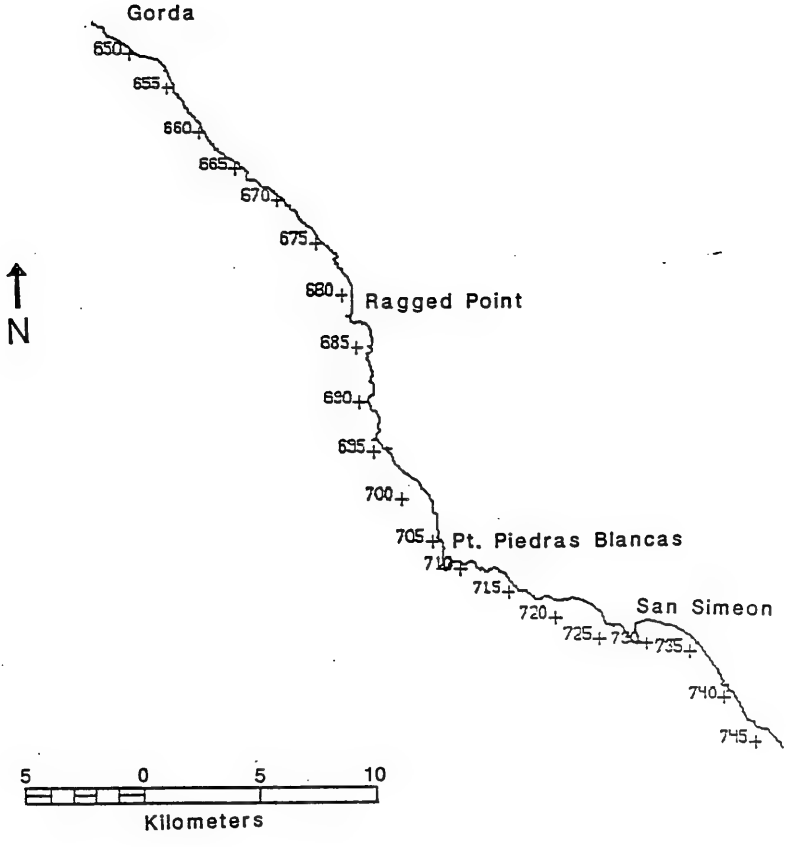


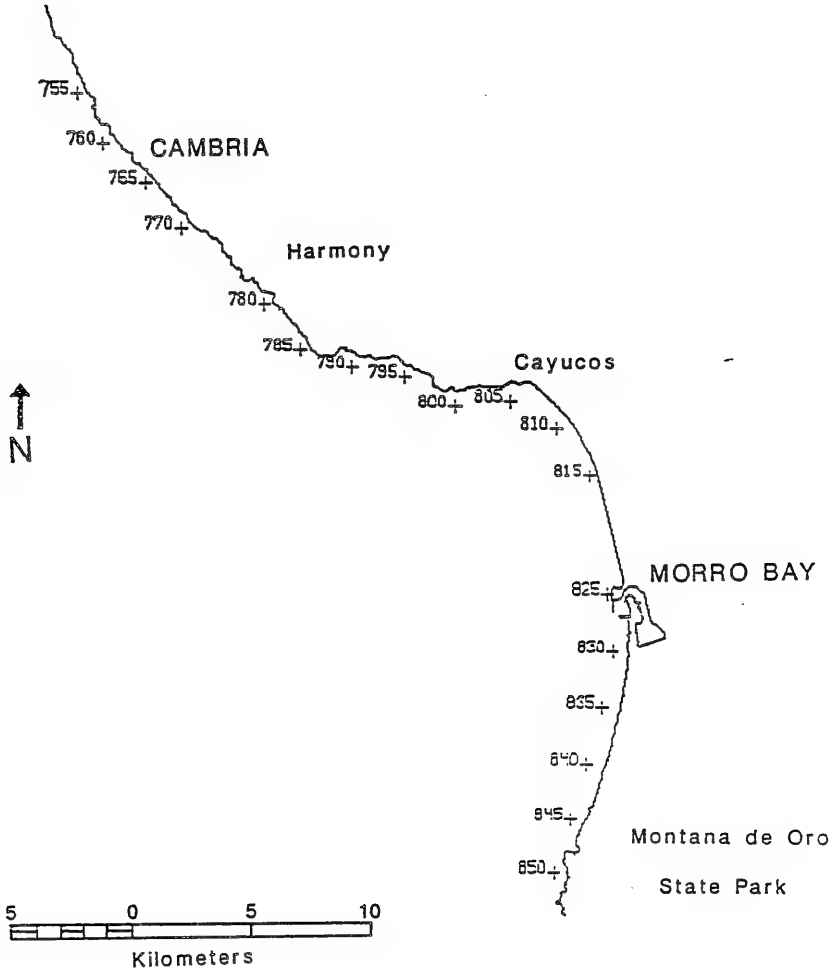
APPENDIX 10.1B -- Ordinates for fathom line along the California coast.

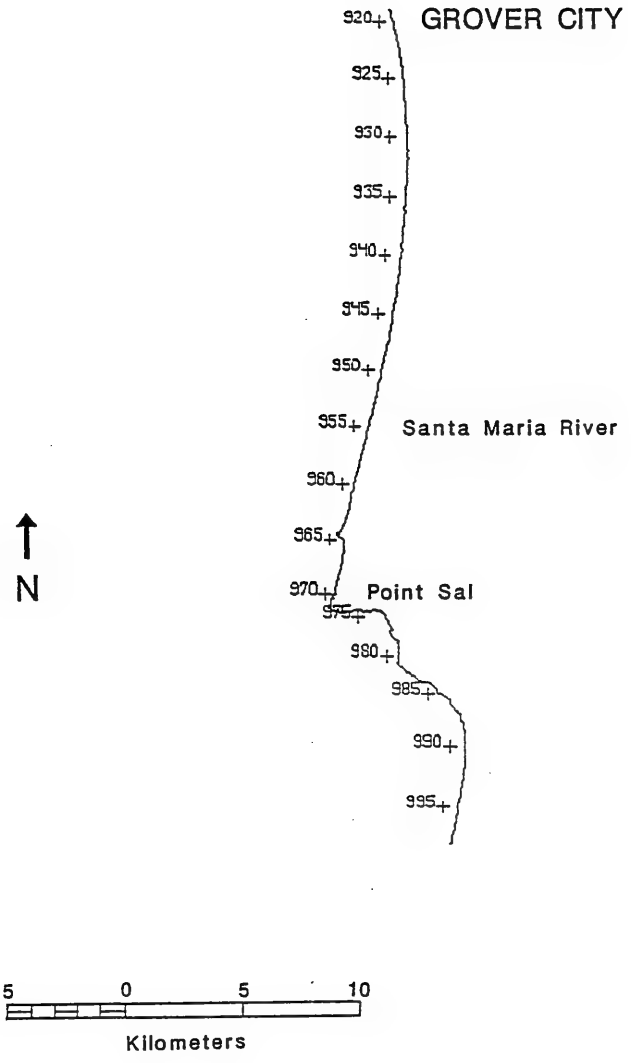


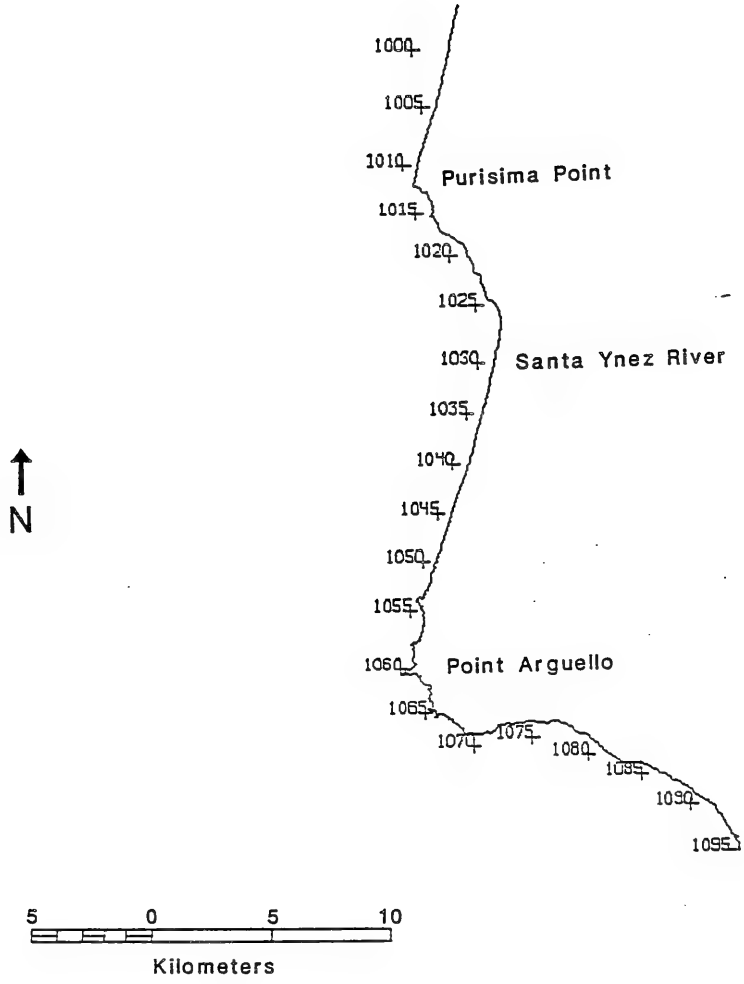

390
385.
380.
395
400
375.
MONTEREY
420
425
CARMEL
430
435
440
Pt. Lobos
445
450
455
460
465
470
475
Notleys Landing
480
485
490
495
Pt. Sur
500
505
510
515
520
Pfeiffer Point
525
530
N
5
0
5
10
Kilometers


540
Grimes Point
545
550
555
560
565
570
John Little State Park
575
580
585
590
Gamboa Point
595
600
605
610
615
620
625
630
635
640
Gorda
N
5
0
5
10
Kilometers


Gorda
650
655
660
665
670
675
680
Ragged Point
685
690
695
700
705
Pt. Piedras Blancas
710
715
720
725
730
735
San Simeon
740
745
N
5 0 5 10
Kilometers


755
760
CAMBRIA
765
770
Harmony
780
785
790
795
Cayucos
800
805
810
815
MORRO BAY
825
830
835
840
845
850
Montana de Oro
State Park
N
5
0
5
10
Kilometers


GROVER CITY
920
925
930
935
940
945
950
955
960
965
970
975
980
985
990
995
Santa Maria River
Point Sal
N
5
0
5
10
Kilometers


1000
1005
1010
Purisima Point
1015
1020
1025
1030
Santa Ynez River
1035
1040
1045
1050
1055
1060
Point Arguello
1065
1070
1075
1080
1085
1090
1095
N
5
0
5
10
Kilometers

APPENDIX 10.2 -- User's Manual for OTPOP: A Simulation Model for Assessing the Risks of Oil Spills to the California Sea Otter Population.

USER'S MANUAL

for

OTPOP

A Simulation Model for Assessing the Risks of Oil Spills to the California Sea Otter Population

1987

University of Minnesota

APPENDIX 10.2 -- User's Manual for OTPOP: A Simulation Model for Assessing the Risks of Oil Spills to the California Sea Otter Population.

I. INTRODUCTION.

This manual provides information only on running OTPOP, it does not explain the logical structure of the model nor the significance of the various parameters. Many problems will be avoided if the user familiarizes his/her self with the model documentation volume before attempting to use the program.

II. TECHNICAL SPECIFICATIONS

Hardware. OTPOP is designed to run on an IBM PC,XT, or AT microcomputer. An Intel 8087 or 80287 coprocessor is required. A hard disk is recommended. A battery operated clock and associated software are necessary for the random number generator.

Software. OTPOP is written in FORTRAN and compiled on the Rand-McFarland IBM Professional FORTRAN Compiler version 1.0. All code is ANSI FORTRAN77 compatible except for 4 IBM Professional extensions used extensively throughout the program: 1) all variables and array elements are automatically set to 0 at the start of the program, 2) some COMMON and declaration statements are included separately in program units through the use of INCLUDE statements, 3) subroutine variables are automatically saved without the use of SAVE statements, and 4) most integer variables are declared as 2 byte (INTEGER*2) to save memory. The action of these extensions must be considered if the program is transported to a different compiler.

The menu screens used to input parameters that are set at runtime are generated using K&S Systems Screen Generator version 4.7. The memory resident portion of the screen generator must be loaded before running OTPOP (this is accomplished in the batch file OP.BAT). If OTPOP is transported to a different compiler a different screen generator interface must be used, or the data entry portion of the program rewritten.

Operating environment. DOS version 3.1 or higher is required as an operating system, and at least 384 kilobytes of RAM must be available. The following statements must be included in the "CONFIG.SYS" file available at boot:

```
DEVICE=ANSI.SYS
BREAK ON
FILES=25
BUFFERS=25
```

The DOS "ANSI.SYS" file must also reside on the boot disk.

III. RUNNING THE PROGRAM

The batch file OT.BAT is supplied to easily load the resident portion of the screen generator, run OTPOP, process the raw output, and restore the proper MODE. To run OT.BAT type "OT" and <enter>. Fig. 1 will briefly appear on the screen as the screen generator is loaded, and Fig. 2, introducing the program, will appear as OTPOP is loaded.

The screens pictured in Figs. 3-10 are used to set run environment and model parameters at runtime. Default values of all parameters automatically appear when the screens are presented. To change a default value move the cursor to the parameter in question and enter the new value. The program automatically checks for parameter values that are out of acceptable range or of the wrong type (for instance, entering a letter when a number is required, or a number with a decimal point when an integer is required). Move back and forth between screens using the F1 and F10 function keys as noted at the bottom of each screen.

Following is a description of the parameters that are set at runtime using the input screens.

Figure 1. K&S Systems copyright notice for the screen n generator.

```
C:\OTTERS\INIPOP>sgx
The Screen Generator v4.47
(C) Copyright 1982,83,84,85 K & S Systems
(C) Copyright 1986 The West Chester Group
PO Box 1304, West Chester, PA 19380, (215) 644-4206
```

Figure 2. Introductory screen for OTPOP.

OTPOP

A SIMULATION MODEL FOR THE ANALYSIS
OF THE RISK OF OIL SPILLS TO THE
CALIFORNIA SEA OTTER POPULATION

FOR
USDI MINERALS MANAGEMENT SERVICE

WRITTEN AT THE
UNIVERSITY OF MINNESOTA

0 1987

Screen 1: Run parameters (Fig. 3):

NUMBER OF YEARS PER RUN. Enter the number of years you want to simulate after the oil spill.

NUMBER OF RUNS WITH OIL SPILL. Enter the number of separate runs of the number of years specified above you want executed.

NUMBER OF CONTROL RUNS. Enter the number of runs you want conducted without introducing an oil spill. The control runs run for the same number of years as the runs with oil spills.

INITIAL POPULATION SIZE. Enter the desired number of independent otters in the simulated population at time of the spill. Because of the stochasticity built in to the model, and because the model runs for 3 simulated years before introducing the spill, the number of animals at the time of the spill may differ slightly from the inputted value. The initial population size will also differ between runs.

DATE OF OIL SPILL. Enter the month (1-12) and day (1-31) to introduce the spill.

DURATION OF SPILL. Enter the number of days (up to 30) that the spill is to affect the population.

NORTH BOUNDARY OF SPILL. Enter the north boundary of the simulated spill using the CDFG 5-fathom ordinate (see Appendix A).

SOUTH BOUNDARY OF SPILL. Enter the south boundary of the simulated spill, using the CDFG 5-fathom ordinate. This value must be greater than the value for the northern boundary entered above.

Figure 3. OTPOP Screen #1 -- Run parameters. Dashed lines indicate location of parameter values edited by user.

SET RUN PARAMETERS:

__ NUMBER OF YEARS PER RUN

___ NUMBER OF RUNS WITH OIL SPILL

___ NUMBER OF CONTROL RUNS

____ INITIAL POPULATION SIZE

__/__ DATE OF OIL SPILL (MONTH/DAY)

__ DURATION OF SPILL

____ NORTH BOUNDARY OF SPILL (<SOUTH)

____ SOUTH BOUNDARY OF SPILL (>NORTH)

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 2: Population parameters (Fig. 4):

EQUILIBRIUM POPULATION SIZE. Enter the carrying capacity, in number of independent otters, of the simulated range. The program OTRANGE may be run separately to determine this value.

NORTH BOUNDARY OF RANGE. Enter the north boundary of the sea otter range at the time of the spill using the CDFG 5-fathom ordinate. Program OTRANGE may be run separately to determine this value.

SOUTH BOUNDARY OF RANGE. Enter the south boundary of the sea otter range at the time of the spill using the CDFG 5-fathom ordinate. This value must be higher than the value entered above for the north boundary of the range. Program OTRANGE may be run separately to determine this value.

MAXIMUM PER CAPITA GROWTH RATE. Enter the maximum attainable per capita annual growth rate of the population, in animals/animal/year. This is "r_{max}" from equation (3) in the documentation volume.

NON-LINEARITY OF DENSITY DEPENDENCE. Enter the value for "b" in equation (3) in the documentation volume. The higher the value of "b" the more rectangular the density dependence function (see Fig. 4 in the documentation volume).

DENSITY INDEPENDENT MORTALITY RATE. Enter the mortality rate, in animals/animal/year, due to density-independent factors. This could be used to simulate incidental gill-net mortality, predation, or harvest ("m" in equation (29) in the documentation volume). See discussion of density independent mortality in the OTRANGE section of the documentation volume.

DEGREE OF COMPENSATION. Enter the proportion of the density independent mortality that will compensate for density dependent mortality. See discussion of density independent mortality in the OTRANGE section of the documentation volume.

* * * * * * * * * * * * * * * *

Note: Density independent growth can be simulated by setting the equilibrium population size very high relative to the initial population size (i.e., at least 10 times as high), and setting the nonlinearity coefficient very high (i.e., 0.05 or greater).

* * * * * * * * * * * * * * * *

Figure 4. OTPOP Screen #2 -- Population parameters. Lines indicate location of parameter values edited by user.

SET POPULATION PARAMETERS:

_____ EQUILIBRIUM POPULATION SIZE

_____ NORTH BOUNDARY OF RANGE (<SOUTH)

_____ SOUTH BOUNDARY OF RANGE (>NORTH)

_____ MAXIMUM PER CAPITA ANNUAL GROWTH RATE

_____ NON-LINEARITY OF DENSITY DEPENDENCE

_____ DENSITY INDEPENDENT MORTALITY RATE

_____ DEGREE OF COMPENSATION

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 3: Survival and reproductive parameters (Fig. 5):

ADULT FEMALE SURVIVAL RATE. Set the annual rate of survival of adult females against incidental risks. This is "a_2" in equation (1) in the documentation volume. Express as a proportion.

MODAL AGE OF FEMALE SENESCENCE. Set the age, in years, of the modal age of death due to old age for females. This is "T" in equation (10) in the documentation volume.

PRIME REPRODUCTIVE RATE. Set the maximum yearly reproductive rate, expressed as weaned females per adult female per year. This is "A" in equation (2) in the documentation volume.

PUP SURVIVAL RATE. Set the proportion of pups that will survive from birth until weaning. Intrauterine mortality is not considered.

ADULT MALE SURVIVAL RATE. Set the annual rate of survival of adult males against incidental risks. This is "a_2" in equation (1) in the documentation volume. Express as a proportion.

MODAL AGE OF MALE SENESCENCE. Set the age, in years, of the modal age of death due to old age for males. This is "T" in equation (10) in the documentation volume.

% VARIATION IN ADULT SURVIVAL. Set the relative percent by which annual adult survival rates may vary. This variance is used only in the recovery phase of the simulation, and the distribution of annual survival rates is assumed to be uniform between the specified boundaries. This simulates the "environmental stochasticity" parameter, "p", described in the description of the structure of LESLIE in the documentation volume.

% VARIATION IN PUP SURVIVAL. Set the relative percent by which annual pup survival rate may vary. This variance is used only in the recovery phase of the simulation, and the distribution of annual survival rates is assumed to be uniform between the specified boundaries. Percent variation in pup survival may differ from percent variation in adult survival.

Figure 5. OTPOP Screen #3 -- survival and reproductive parameters.
Lines indicate location of parameter values edited by user.

SET SURVIVAL & REPRODUCTIVE PARAMETERS:

_____ ADULT FEMALE SURVIVAL RATE

_____ MODEL FEMALE AGE OF SENESCENCE

_____ PRIME REPRODUCTIVE RATE

_____ PUP SURVIVAL RATE

_____ ADULT MALE SURVIVAL RATE

_____ MODEL MALE AGE OF SENESCENCE

±_____ PERCENT VARIATION IN ADULT SURVIVAL

±_____ PERCENT VARIATION IN PUP SURVIVAL

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 4: Movement parameters (Fig. 6):

Classes of animals are listed down the left side of the screen, movement parameters along the top. AR is the autoregressive parameter, CE is the displacement parameter, SIGMA is the standard deviation of daily distance moved, and VMAX is the maximum possible daily distance moved. See the discussion of the structure of OTMOVE and equation (22) in the documentation volume.

Figure 6. OTPOP Screen #4 -- Movement parameters. Lines indicate location of parameter values edited by user.

SET OTTER MOVEMENT PARAMETERS:

	AR	CE	SIGMA	VMAX
JUVENILE FEMALES	_____	_____	_____	_____
ADULT FEMALES W/PUP	_____	_____	_____	_____
ADULT FEMALE W/O PUP	_____	_____	_____	_____
JUVENILE MALES	_____	_____	_____	_____
ADULT NON-TERRITORIAL MALES	_____	_____	_____	_____
ADULT TERRITORIAL MALES	_____	_____	_____	_____

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 5: Male territoriality parameters (Fig. 7):

AGE AT WHICH POTENTIALLY TERRITORIAL. Enter the age, in years, at which males may hold breeding territories.

MAXIMUM % OF POTENTIALS THAT HOLD TERRITORIES. Enter the percent of potentially territorial males that will hold territories at the height of the breeding season.

MINIMUM % OF POTENTIALS THAT HOLD TERRITORIES. Enter the minimum percent of potentially territorial males that will hold territories at any time throughout the year.

MEAN TERRITORY LENGTH. Enter the average length of a male territory, measured along the 5-fathom line, in 1/2 km units.

S. D. OF TERRITORY LENGTH. Enter the standard deviation around mean territory length, in 1/2 km units.

MEAN ARRIVAL DATE. Enter the average date (month (1-12) / day (1-31)) of arrival on a territory.

S. D. OF ARRIVAL DATE. Enter the standard deviation, in days, of average arrival date.

MEAN DEPARTURE DATE. Enter the average date (month (1-12) / day (1-31)) of departure from a territory.

S. D. OF DEPARTURE DATE. Enter the standard deviation, in days, of average departure date.

* * * * * * * * * * * * * * * * * *

Note: The seasonality of territorial behavior and migrations can be controlled through the standard deviations of arrival and departure dates. Large standard deviations lead to less pronounced seasonality. See discussion in the migratory movements by adult males section of the documentation volume.

Figure 7. OTPOP Screen #5 -- Male territoriality parameters.
Lines indicate location of parameter values edited by user.

SET MALE TERRITORIALITY PARAMETERS:

__	AGE AT WHICH POTENTIALLY TERRITORIAL
_____	MAXIMUM % OF POTENTIALS THAT HOLD TERRITORIES
_____	MINIMUM % OF POTENTIALS THAT HOLD TERRITORIES
_____	MEAN TERRITORY LENGTH
_____	S.D. OF TERRITORY LENGTH
__/__	MEAN ARRIVAL DATE (MONTH/DAY)
___	S.D. OF ARRIVAL DATE (IN DAYS)
__/__	MEAN DEPARTURE DATE (MONTH/DAY)
___	S.D. OF DEPARTURE DATE (IN DAYS)

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 6: Oil spill response parameters (Fig. 8):

Columns 1 and 5 show the day of the oil spill, columns 2 and 6 list the probabilities of mortality after contact with the spill for each day, columns 3 and 7 list the probabilities of locally avoiding a spill on each day, and columns 4 and 8 list the probabilities of avoiding a spill by shifting the location of the home range on each day of the spill. Parameters for days greater than the duration of spill set in screen 1 are ignored by the program. See discussion of the structure of OTMOVE in the documentation volume.

Figure 8. OTPOP Screen #6 -- Oil spill response parameters. Lines indicate location of parameter values edited by user.

SET DAILY PROBABILITIES OF MORTALITY, AVOIDANCE, AND EMIGRATION DURING EXPOSURE TO OIL SPILL:

DAY	P(MORT)	P(AVOID)	P(EMIG))	DAY	P(MORT)	P(AVOID)	P(EMIG)
1	_____	_____	_____	16	_____	_____	_____
2	_____	_____	_____	17	_____	_____	_____
3	_____	_____	_____	18	_____	_____	_____
4	_____	_____	_____	19	_____	_____	_____
5	_____	_____	_____	20	_____	_____	_____
6	_____	_____	_____	21	_____	_____	_____
7	_____	_____	_____	22	_____	_____	_____
8	_____	_____	_____	23	_____	_____	_____
9	_____	_____	_____	24	_____	_____	_____
10	_____	_____	_____	25	_____	_____	_____
11	_____	_____	_____	26	_____	_____	_____
12	_____	_____	_____	27	_____	_____	_____
13	_____	_____	_____	28	_____	_____	_____
14	_____	_____	_____	29	_____	_____	_____
15	_____	_____	_____	30	_____	_____	_____

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 7: RUNID (Fig. 9):

Enter character string of up to 6 characters that will be used to identify the output from the current model run. This identification string will appear at the top of the .LOG file and on output from PROC. Different RUNID strings should be used for every production run of the model to ensure that output\ files from a particular run may be permanently associated with the appropriate .LOG file.

Figure 9. OTPOP Screen #7 -- Set run identification string. Lines indicate location of parameter values edited by user.

ENTER SIX CHARACTER RUN IDENTIFICATION STRING:

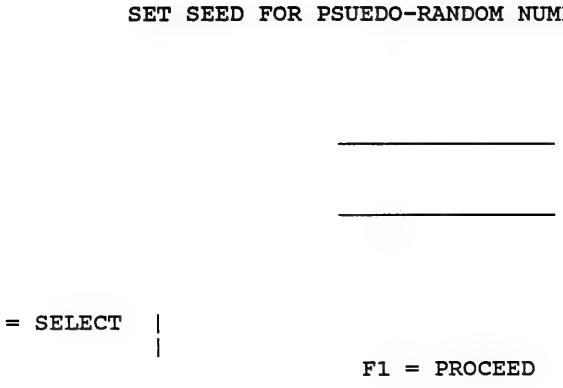
_____

F1 = PROCEED
F10 = PREVIOUS SCREEN

Screen 8: Set seed for random number generator (Fig. 10):

Toggle back and forth between "Use constants" and "Use clock" with the cursor arrow keys. The same integers will be used as random number seeds on every run that is initiated by using constants -- this is supplied as a testing or debugging aid as it ensures that the same sequence of random numbers will be used in each run. The clock should be used to set the random number seeds for production runs.

Figure 10. OTPOP Screen #8 -- Set random number generator seed.



After all screens have been examined and parameters set the model will begin execution. Parameter values used in the current run will be recorded in the OTPOP.LOG file once the model begins execution. To terminate the program prematurely at any time press <control> and <break> simultaneously (since the program will break only during input or output operations it may be several seconds to a few minutes before the program terminates after pressing <control><break>).

IV. REQUIRED FILES.

Several files are required to reside on the same disk and subdirectory for the program to function correctly. They are:

MAINPOP.EXE	(OTPOP program execution module)
PROC.EXE	(Data processing execution module)
SGX.EXE	(Loads memory-resident portion of screen generator)
MODE.COM	(Restores correct mode after execution)
OP.BAT	(Batch file to execute above programs)
PARASC	(Screen generator library)
PROFORT.ERR	(Error messages for IBM Professional FORTRAN)
ZSCORES.DAT	
DFLT.DAT	
CDIST.DAT	
SR.DAT	
SBST.DAT	

Files with the .DAT extension are data files that are read in during program execution. ZSCORES.DAT contains values of the standard normal distribution and should not be disturbed. The remainder of the .DAT files may be edited by the user using a standard word processor. If these files are edited, the edited files must be saved as ASCII text files under their original names.

DFLT.DAT contains the default values of the parameters set at runtime. Parameter values are in list format, with 1 space separating each value. The values are listed in the order they appear on the screens (Fig. 11).

CDST.DAT contains the density functions for summer and winter used in the distribution algorithms of the model. They should be derived from the most recent USFWS/CDFG census data. The file consists of 5 columns in list format, with a space separating the columns (Fig. 12). The first column is an integer representing each 1/2 kilometer segment of the 5-fathom ordinate system. The second column is the proportion of the population that was observed in that segment of the range during the most recent spring/summer census. The third column indicates the method by which that section of the coast was counted ("0" = from ground, "1" = by air) for that census. The fourth column is the proportion of the population that was observed in that segment of the range during the most recent fall/winter census. The fifth column indicates the method by which that section of the coast was counted ("0" = from ground, "1" = by air) for that census.

The digitizing program used by USFWS to enter the census data will produce files in the correct format that can be

Figure 11. Part of the DFLT.DAT file.

```
 10 1 1 1500 1 1 1 201 955
1500 201 955 0.0900 0.0050 0.0000 1.0000
0.9300 15.000 0.2500 0.5300 0.8700 9.0000 5.0 5.0
0.36700  -0.1630  8.09000  37.5000
-0.0250  -0.4060  6.39000  37.5000
-0.0090  -0.7060  2.95000  08.4000
-0.0450  -0.2900  8.56000  48.9000
00.1050  -0.8150  4.64000  48.9000
00.0420  -1.0440  1.93000  48.9000
6 60 20 8.1100 0.4400 5 23 11 12 1 15
 1 1.0000 0.0000 0.0000
 2 1.0000 0.0000 0.0000
 3 1.0000 0.0000 0.0000
 4 1.0000 0.0000 0.0000
 5 1.0000 0.0000 0.0000
 6 1.0000 0.0000 0.0000
 7 1.0000 0.0000 0.0000
 8 1.0000 0.0000 0.0000
 9 1.0000 0.0000 0.0000
10 1.0000 0.0000 0.0000
11 1.0000 0.0000 0.0000
12 1.0000 0.0000 0.0000
13 1.0000 0.0000 0.0000
14 1.0000 0.0000 0.0000
15 1.0000 0.0000 0.0000
16 1.0000 0.0000 0.0000
17 1.0000 0.0000 0.0000
18 1.0000 0.0000 0.0000
19 1.0000 0.0000 0.0000
20 1.0000 0.0000 0.0000
21 1.0000 0.0000 0.0000
22 1.0000 0.0000 0.0000
```

Figure 12. Part of the CDST.DAT file.

```
202 0 1 0 1
203 0 1 0 1
204 0 1  0.00041 1
205  0.00123 1 0 1
206 0 1 0 1
207  0.00041 1 0.00039 1
208 0 1 0 1
209 0 1 0 1
210 0 1 0 1
211  0.00041  1 0 1
212 0 1 0 1
213 0 1 0 1
214 0 1 0 1
215 0 1 0 1
216 0 1 0 1
217 0 1 0 1
218 0 1 0 1
219 0 1 0 1
220 0 1 0 1
221 0 1 0 1
222  0.00041 1 0 1
223 0 1 0 1
224 0 1 0 1
225 0 1 0 1
```

copied onto the appropriate disk after each census to keep the model input data updated.

SR.DAT contains sex ratio data for the sea otter range, used in the distribution algorithms of the model. Sex ratios are recorded by CDFG carcass recovery area. The file consists of 3 columns, in list format, with spaces separating the columns (Fig. 13). The first column contains an integer representing the northern boundary of the segment in the 5-fathom line ordinate system, the second column contains the number of males per female in the segment during the spring/summer, the third column contains the number of males per female in the segment during fall/winter.

SBST.DAT contains codes for the substrate along the coast. Substrate is either rock or sand. The file consists of 2 columns, in list format, single spaces separating the columns (Fig. 14). The first column is an integer representing a point along the 5-fathom line ordinate system where the substrate changes from one to the other, the second column represents the substrate of the area south of the point to the next point where the substrate changes. A "1" represents rock substrate, a "0" represents sand substrate. This file was coded from U.S. Geological Survey topographic maps, and should not have to be changed.

Figure 13. Part of the SR.DAT file.

```
201         4.5         16.7
216         4.5         16.7
229         4.5         16.7
256         4.5         16.7
271         4.5         16.7
321         1     3
366         0.5         0.88
377         0.5         0.88
384         0.5         0.88
390         0.33         0.33
400         0.33         0.33
411         0.43         0.43
430         0.43         0.43
449         0.5         0.44
473         0.5         0.44
499         0.5         0.44
524         0.5         0.44
599         0.5         0.44
640         0.41         0.37
668         0.41         0.37
694         0.41         0.37
730         0.33         0.30
753         0.33         0.30
787         0.82         0.61
806         0.82         0.61
825         0.82         0.61
844         1.0          3.0
853         1.0          3.0
891         4.5         16.7
916         4.5         16.7
942         4.5         16.7
989         4.5         16.7
999         5.          17.
```

Figure 14. Part of the SBST.DAT file.

```
 199      0
 378      1
 421      0
 426      1
 466      0
 468      1
 489      0
 497      1
 680      0
 682      1
 722      0
 723      1
 730      0
 732      1
 740      0
 742      1
 746      0
 750      1
 815      0
 843      1
 894      0
 896      1
 914      0
 963      1
 966      0
 970      1
 977      0
 978      1
 979      0
 981      1
 989      0
1007      1
```

V. RAW OUTPUT FILES.

Seven files are generated as output from OTPOP. OTPOP.LOG is a log file, giving the date and time of execution, and the values of the parameters set at runtime (Fig. 15). RUNID.DAT will contain the run identification string. The other 5 files are output data files, containing the raw results of the simulations. Program PROC is used to process and summarize the raw output data.

NTS.DAT contains the simulated population sizes for runs with an oil spill. There are 5 columns; the first gives the run number, the second gives the year (the oil spill always occurs in year 0, so that the years simulated before the spill are designated -3,-2,-1). Year 0 will be recorded twice for each run, once for just before the simulated spill, once for just after the spill. The third, fourth, and fifth columns give the number of independent females, number of independent males, and number of pups, respectively, for that year during the month of the spill (Fig. 16).

NTC.DAT is exactly the same as NTS.DAT, but contains data for the control (without oil spill) runs, so year 0 wil be recorded only once for each run.

DTS.DAT contains the total numbers of animals killed by the simulated spills. There are 13 columns; the first gives the run number, the next 6 pairs of columns give the number of animals and the proportion of the population killed for each of the 6 classes of animals (see discussion of the structure of OTMOVE in the documentation volume) respectively (Fig. 17).

DDS.DAT contains the numbers of animals killed by the simulated spills on a daily basis. It has 8 columns; the first gives the run number, the second gives the day of the spill, and the third through eighth give the numbers of animals of classes 1-6 (see discussion of the structure of OTMOVE in the documentation volume) killed on that particular day (Fig. 18).

RVS.DAT contains the population's reproductive value (see discussion of model output in documentation volume) before and after the simulated spill. It has 3 columns, the first giving the run number, the second giving the population reproductive value just before the spill, and the third giving the population reproductive value just after the spill (Fig. 19).

RCS.DAT contains the recovery times for population. It has 3 columns. The first gives the run number, the second gives the population size just prior to the spill, and the third gives the number of years simulated before that

Figure 15. The OTPOP.LOG file.

```
FOLLOWING ARE RUNTIME INPUTS FOR RUNIL:
          EXAMP1

DATE -- 9/ 4/87      TIME -- 22:54

  DATE AND TIME USED TO GENERATE RANDOM NUMBER SEEDS
10,"NUMBER OF YEARS PER RUN"
 10,"NUMBER OF RUNS WITH OIL SPILL"
 10,"NUMBER OF CONTROL RUNS"
1000,"INITIAL POPULATION SIZE"
 1,"MONTH OF SPILL"
 1,"DAY OF SPILL"
 1,"DURATION OF SPILL
 345,"NORTH BOUNDARY OF SPILL"
 400,"SOUTH BOUNDARY OF SPILL"
1000,"EQUILIBRIUM POPULATION SIZE"
 201,"NORTH BOUNDARY OF RANGE"
 955,"SOUTH BOUNDARY OF RANGE"
 0.090,"MAXIMUM PER CAPITA ANNUAL GROWTH RATE"
 0.005,"NON-LINEARITY OF DENSITY DEPENDENCE"
 0.000,"DENSITY INDEPENDENT MORTALITY RATE"
 1.000,"DEGREE OF COMPENSATION"
 0.930,"ADULT FEMALE SURVIVAL RATE"
15.000,"MODAL AGE OF FEMALE SENESCENCE"
 0.250,"PRIME REPRODUCTIVE RATE"
 0.530,"PUP SURVIVAL RATE"
 0.870,"ADULT MALE SURVIVAL RATE"
 9.000,"MODAL MALE AGE OF SENESCENCE"
 5.000,"PERCENT VARIATION IN ADULT SURVIVAL"
 5.000,"PERCENT VARIATION IN PUP SURVIVAL"
 "","AR","CE","SIGMA","VMAX"
 "JUVENILE FEMALES" 0.367-0.163 8.09037.500
 "ADULT FEMALES W/PUP"-0.025-0.406 6.39037.500
 "ADULT FEMALES W/O PUP"-0.009-0.706 2.950 8.400
 "JUVENILE MALES"-0.045-0.290 8.56048.900
 "ADULT NON-TERRITORIAL MALES" 0.105-0.815 4.64048.900
 "ADULT TERRITORIAL MALES" 0.042-1.044 1.93048.900
  6,"AGE AT WHICH POTENTIALLY TERRITORIAL"
 60.000,"MAXIMUM % OF POTENTIALS THAT HOLD TERRITORIES"
 20.000,"MINIMUM % OF POTENTIALS THAT HOLD TERRITORIES"
  8.110,"MEAN TERRITORY LENGTH"
  0.440,"S.D. OF TERRITORY LENGTH"
  5,"MEAN ARRIVAL DATE MONTH"
 23,"MEAN ARRIVAL DATE DAY"
  11,"S.D. OF ARRIVAL DATE IN DAYS"
 12,"MEAN DEPARTURE DATE MONTH"
  1,"MEAN DEPARTURE DATE DAY"
  15,"S.D. OF DEPARTURE DATE IN DAYS"
 "DAY","P(MORTALITY)","P(AVOIDANCE)","P(EMIGRATION)"
 1 1.000 0.000 0.000
```

Figure 16. Part of the NTS.DAT file.

```
1        1        593        361        130
1        2        591        367        126
1        3        590        368        127
1        4        617        358        124
1        5        641        376        138
1        6        622        368        120
1        7        599        345        122
1        8        597        347        118
1        9        578        335        121
1       10        579        327        125
2       -4        647        352        101
2       -3        630        343        128
2       -2        630        331        137
2       -1        632        348        131
2        0        644        337        117
2        0        597        324        108
2        1        607        310        137
2        2        623        344        130
2        3        624        340        114
2        4        621        322        137
2        5        650        346        121
2        6        673        331        142
2        7        676        350        143
2        8        666        366        132
2        9        656        351        138
2       10        664        355        140
3       -4        647        352        105
3       -3        659        355        130
3       -2        666        366        129
3       -1        658        371        121
3        0        662        350        118
3        0        621        330        111
3        1        635        332        119
3        2        645        340        142
3        3        623        337        132
3        4        626        345        123
3        5        624        322        132
3        6        630        337        123
3        7        645        321        121
3        8        637        327        130
3        9        654        325        114
3       10        654        319        138
4       -4        647        352        122
4       -3        653        336        148
4       -2        669        318        137
4       -1        668        325        133
```

Figure 17. Part of the DTS.DAT file.

1	3	0.020	10	0.045	17	0.093	39	0.083	16	0.122	85	0.073
2	6	0.040	7	0.037	12	0.071	35	0.074	9	0.077	69	0.063
3	6	0.043	14	0.066	15	0.079	26	0.055	7	0.059	68	0.060
4	11	0.073	11	0.064	13	0.070	32	0.065	11	0.089	78	0.070
5	3	0.019	7	0.031	15	0.080	41	0.083	8	0.065	74	0.062
6	7	0.044	9	0.044	15	0.083	43	0.090	12	0.102	86	0.076
7	2	0.012	4	0.020	18	0.105	33	0.070	7	0.060	64	0.057
8	10	0.061	11	0.050	16	0.101	44	0.098	11	0.102	92	0.084
9	3	0.017	12	0.057	6	0.039	34	0.071	11	0.083	66	0.057
10	9	0.057	11	0.052	13	0.068	32	0.067	10	0.074	75	0.064

Figure 18. Part of the DDS.DAT file.

```
 1   1     3    7   3    17   23   16
 2   1     6    5   2    12   26    9
 3   1     6   13   1    15   19    7
 4   1    11   10   1    13   21   11
 5   1     3    4   3    15   33    8
 6   1     7    8   1    15   31   12
 7   1     2    1   3    18   26    7
 8   1    10    9   2    16   33   11
 9   1     3   10   2     6   23   11
10   1     9    9   2    13   22   10
```

Figure 19. Part of the RVS.DAT file.

```
 1    820.5      749.6
 2    819.9      761.1
 3    829.4      781.5
 4    861.8      807.8
 5    856.5      788.0
 6    829.5      753.2
 7    800.4      739.0
 8    762.9      691.9
 9    807.1      755.7
10    859.6      802.3
```

population size was reached again (Fig. 20). For simulations in which the population never attained pre-spill size the time to recovery is recorded as a negative number.

Figure 20. Part of the RCS.DAT file.

```
 1   1158   -10
 2   1098     5
 3   1130   -10
 4   1121   -10
 5   1191   -10
 6   1139     8
 7   1131   -10
 8   1099     9
 9   1152   -10
10   1176   -10
```

VI. PROCESSING RAW OUTPUT DATA

Raw output data are summarized using the FORTRAN program PROC and LOTUS123. PROC is run automatically by the batch file OP.BAT after MAINPOP finishes execution. It produces a summary of the run (Fig. 21) in the file "OTPOP.RPT". At the top of OTPOP.RPT the RUNID identification string is given. Following is a summary of the control runs listing the year and the number of independent females, independent males, and dependent pups in the population. In parentheses after each of these are given the range and standard deviations of the population sizes in each year.

Following the summary of the control runs is a summary of the oil spill runs, in the same format. Year "-0" is just prior to the spill, year "+0" is just after the spill.

Following that is a summary of the total number of deaths from the oil spill, and a summary of the recovery after the spill.

Besides OTPOP.RPT, PROC generates 3 files, "NO_SPILL.DAT", "DEATHS.DAT", and "SPILL.DAT", that can be used by LOTUS123 to produce rough graphs of the model output. A LOTUS macro, "OT123.WK1" is supplied. It is expected that you have a general understanding of the LOTUS123 package (including PrintGraph) in order to use the macro.

Files "SPILL.PIC", "NO_SPILL.PIC", "COMPARE.PIC", and "DEATHS.PIC" are supplied with "OT123.WK1" and must be present in order for the macro to run. To run the macro, run Lotus 123 and then retrieve [/FR] the worksheet OT123.WK1 in the usual manner (see your LOTUS123 manual for details). At this point you may invoke the macro by keying [alt]G. As the macro runs, 4 graphs will be displayed on the screen. The macro will pause while displaying each graph and you will be required to depress the space bar in order to proceed with the execution of the macro.

After the macro has been executed successfully the 4 above mentioned picture files (*.PIC) will be created. In addition to these newly created files, the graphs will be named in the current worksheet. If you wish to keep this information, save the current worksheet OT123.WK1 under a new name. From this point, you may wish to modify the graphs using the LOTUS123 /Graph menus and save modified graphs in new .PIC files. For information on how to create or modify graphs consult your LOTUS123 manual.

The first graph (NO_SPILL.PIC) produced by the macro traces the mean total independent population size through each year of the control simulations (Fig. 22). The lines on

OUTPUT FOR RUNID EIAMP1

CONTROL RUNS:

YEAR	FEMALES			MALES			PUPS		
-4	647.0(647- 647,	0.0)		352.0(352- 352,	0.0)		120.1(106- 129,	6.4)	
-3	636.6(622- 647,	6.3)		349.5(333- 361,	8.2)		135.0(123- 152,	7.3)	
-2	640.4(624- 651,	8.3)		352.1(331- 372,	14.0)		131.0(115- 149,	9.7)	
-1	644.6(622- 667,	15.4)		353.7(345- 377,	9.5)		126.5(117- 139,	7.3)	
0	640.8(597- 666,	21.8)		354.8(317- 376,	18.4)		127.3(102- 142,	11.8)	
1	639.5(599- 659,	19.0)		345.2(328- 385,	16.8)		126.5(112- 135,	7.2)	
2	632.8(601- 661,	20.9)		363.4(327- 390,	20.2)		126.1(112- 148,	10.2)	
3	624.9(592- 661,	19.5)		358.7(330- 383,	18.5)		126.7(113- 141,	8.7)	
4	625.0(602- 672,	16.1)		356.5(320- 393,	21.1)		130.9(119- 141,	7.2)	
5	630.5(604- 667,	16.4)		348.9(321- 387,	24.0)		126.1(110- 138,	9.6)	
6	637.3(602- 676,	21.2)		341.3(315- 376,	18.0)		127.1(117- 138,	6.1)	
7	637.4(602- 663,	18.8)		345.2(315- 371,	18.6)		127.7(116- 139,	6.4)	
8	640.9(608- 688,	22.8)		345.8(313- 376,	18.2)		130.3(111- 152,	12.3)	
9	645.4(625- 676,	15.3)		348.6(304- 401,	25.5)		134.8(121- 153,	10.6)	
10	648.8(631- 669,	13.9)		352.7(315- 385,	19.0)		131.4(123- 142,	5.1)	

OIL SPILL RUNS:

YEAR	FEMALES			MALES			PUPS		
-4	647.0(647- 647,	0.0)		352.0(352- 352,	0.0)		117.9(101- 128,	8.5)	
-3	642.8(621- 659,	13.1)		348.1(333- 364,	8.6)		137.1(125- 154,	9.4)	
-2	646.7(610- 669,	17.4)		354.8(318- 380,	18.8)		129.6(117- 137,	6.5)	
-1	650.9(615- 668,	16.3)		360.8(325- 382,	17.7)		130.1(117- [illegible]	6.1)	
-0	652.2(608- 680,	20.5)		364.9(323- 387,	[illegible])		122.4(108- 135,	8.2)	
+0	602.3(548- 629,	23.0)		349.3([illegible]- 377,	22.9)		112.2(97- 125,	7.6)	
1	605.7(551- 633,	28.[illegible])		347.6(310- 379,	22.4)		118.4(104- 137,	9.3)	
2	[illegible](577- 651,	24.5)		348.5(324- 369,	14.9)		121.0(109- 142,	9.5)	
3	616.8(581- 654,	19.9)		345.4(329- 372,	15.5)		120.7(108- 132,	7.5)	
4	624.3(607- 643,	12.1)		338.6(322- 362,	13.9)		126.8(113- 137,	7.2)	
5	630.2(595- 650,	16.2)		343.2(305- 387,	23.3)		126.4(121- 138,	5.2)	
6	635.4(616- 673,	17.8)		338.0(299- 368,	19.2)		129.7(120- 142,	6.3)	
7	639.3(599- 676,	21.4)		334.8(314- 352,	13.8)		127.5(118- 143,	7.6)	
8	642.5(597- 673,	24.9)		330.7(298- 366,	21.2)		127.4(118- 141,	6.6)	
9	649.1(578- 678,	28.0)		330.8(305- 351,	14.3)		129.2(114- 141,	8.8)	
10	650.9(579- 681,	26.2)		333.5(297- 355,	18.9)		134.7(123- 147,	7.4)	

NUMBER OF DEATHS FROM OIL SPILL:

CLASS	MEAN	S.D.	RANGE	PERCENT OF POPULATION MEAN	S.D.	RANGE
JUVENILE MALES	6.0	3.1	2 - 11	3.86	1.99	1.20 7.30
ADULT MALES	9.6	2.8	4 - 14	4.66	1.37	2.00 6.60
JUVENILE FEMALES	14.0	3.2	6 - 18	7.89	1.80	3.90 10.50
ADULT FEMALES	35.9	5.4	26 - 44	7.56	1.22	5.50 9.80
PUPS	10.2	2.6	7 - 16	8.33	1.96	5.90 12.20
TOTAL ANIMALS	75.7	9.0	64 - 92	6.66	0.84	5.70 8.40

RECOVERY AFTER OIL SPILL:

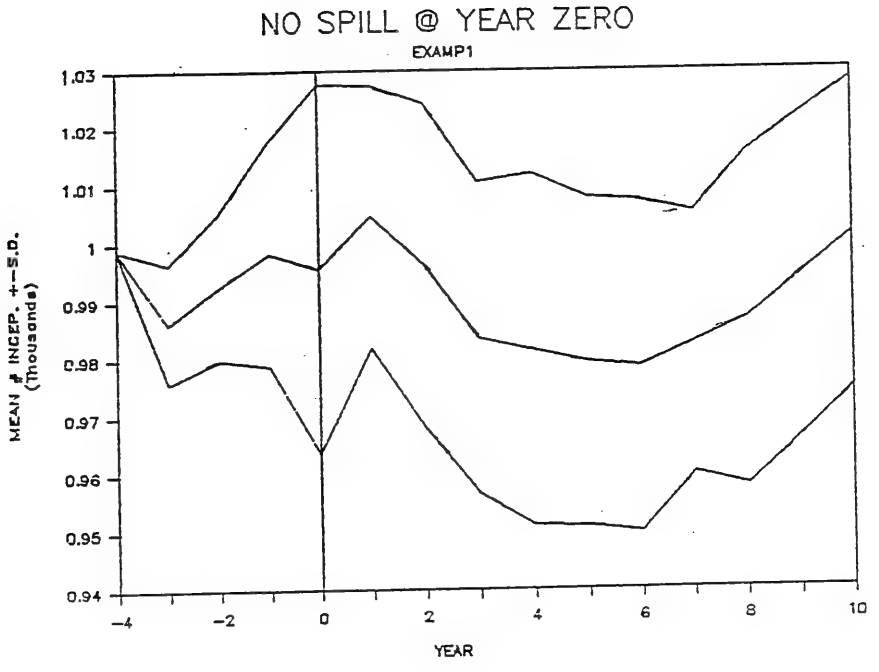
	MEAN	S.D.	RANGE
REPRODUCTIVE VALUE BEFORE SPILL	824.8	29.0	762.9- 861.8
REPRODUCTIVE VALUE AFTER SPILL	763.0	32.4	691.9- 807.8
REPRODUCTIVE VALUE REDUCTION (%)	7.506	1.19617	5.775- 9.307
YEARS TO RECOVERY	7.333	1.69967	5.000- 9.000

IT ON 7 OF 10 RUNS (70.0%) THE POPULATION
DID NOT RECOVER TO PRE-SPILL SIZE

TIME TO RECOVERY CALCULATED ONLY FOR RUNS THAT DID RECOVER.

Figure 21. The OTPOP.RPT file generated by PROC.

Figure 22. Population sizes through each year of control simulations.



either side of the mean trace the range of population sizes that occurred during the simulations. The second graph (SPILL.PIC) traces the oil spill simulations in the same format as NO_SPILL.PIC (Fig. 23). The third graph (COMPARE.PIC) plots the means from both the control and the oil spill runs on the same graph, allowing visual comparison of the population trajectories (Fig. 24). The last graph (DEATH.PIC) traces the mean cumulative number of deaths due to oil spill on each day of the spill (Fig. 25).

If you wish to modify the macro or just want to see the macro depress the [End] then the [Home] key and you will move to the far end of the worksheet, where the macro is located. If you wish to modify the macro we suggest that you first make a copy of it in case you need to refer to the original while editing.

Figure 23. Population sizes during oil spill simulations.

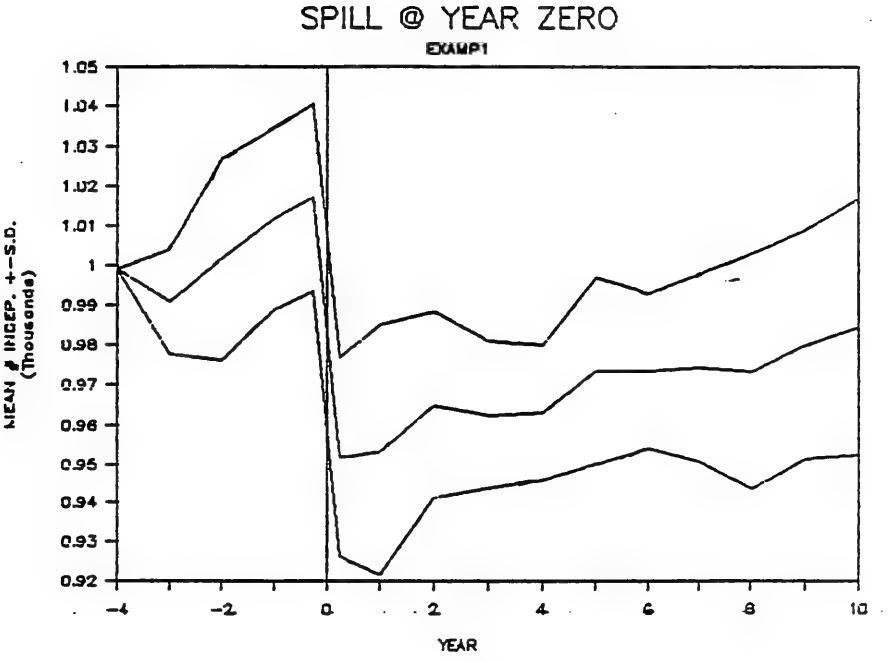


Figure 24. Plot of control population and oil spill population for simulations.

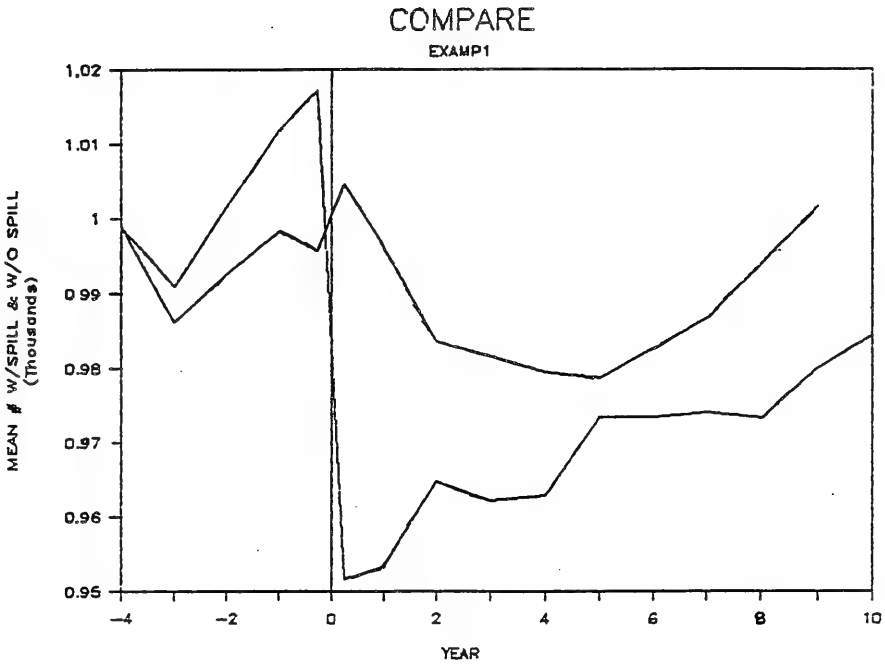
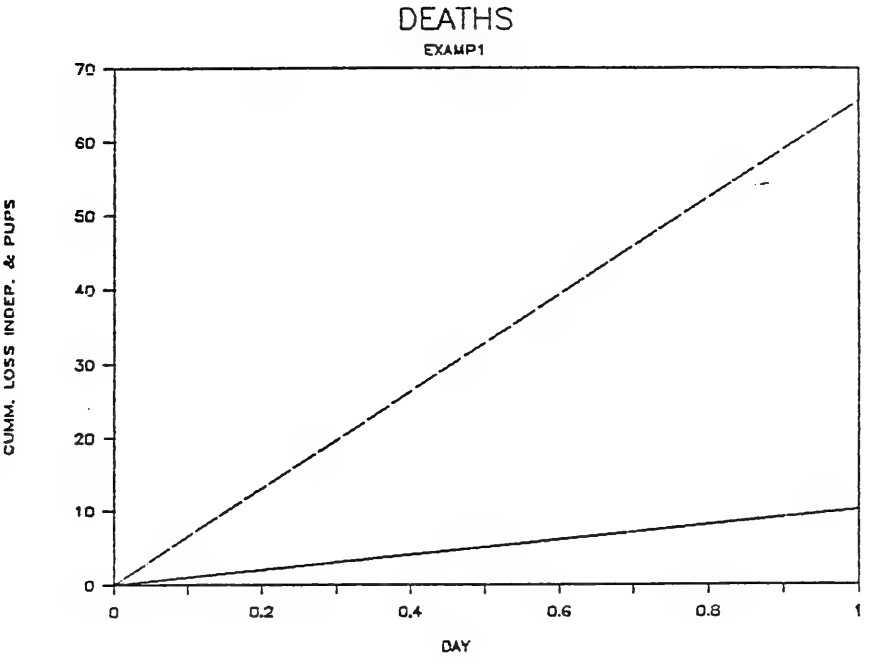


Figure 25. Cumulative deaths due to oil spill.



VII. ERRORS.

Errors in model runs can occur at 3 levels. Screen generator errors occur when values out of range or of the wrong type are input. The program will warn you of the error and it can be corrected by simply typing in an acceptable value. A screen generator error will also occur if the SGX interface has not been loaded prior to running the model, or if the screen library PARASC is not available.

IBM Professional FORTRAN runtime errors can occur when the program is unable to execute a program statement. For instance, if one of the input .DAT files is missing, incomplete, or in the wrong format. The error messages are generated from the PROFORT.ERR file, and will be noted on the screen. These messages may often be cryptic. If a PROFORT message indicates a unit or input error, check that all input files are present and in the correct format. Other situations that may lead to PROFORT runtime errors occur when impossible mathematical operations are attempted, such as division by 0 or taking the log of a negative number. Usually this will occur when an unrealistic combination of parameter values have been input. The error may or may not be fatal to program execution, but even if the program continues to run the output will be suspect.

Program error trapping is the third level of possible error. Because there are so many possible combinations of parameter values that can be set, it has been impossible to build in complete logical error-trapping, but the program does check for many impossible combinations, such as setting survival rates too low to achieve specified growth rates, or setting pup survival rate too low to achieve the specified reproductive rate. Should an error occur on this level the program will terminate and you should correct the parameter values in the next run.

The program is extremely complex, and it is very likely that errors not described herein may occur. No program of this size can ever be guaranteed to be bug-free. Should you not be able to correct an error, be sure to save the log file and all input files, and any output files generated during the run. Notify Allan Brody or Don Siniff and send copies of the saved files.

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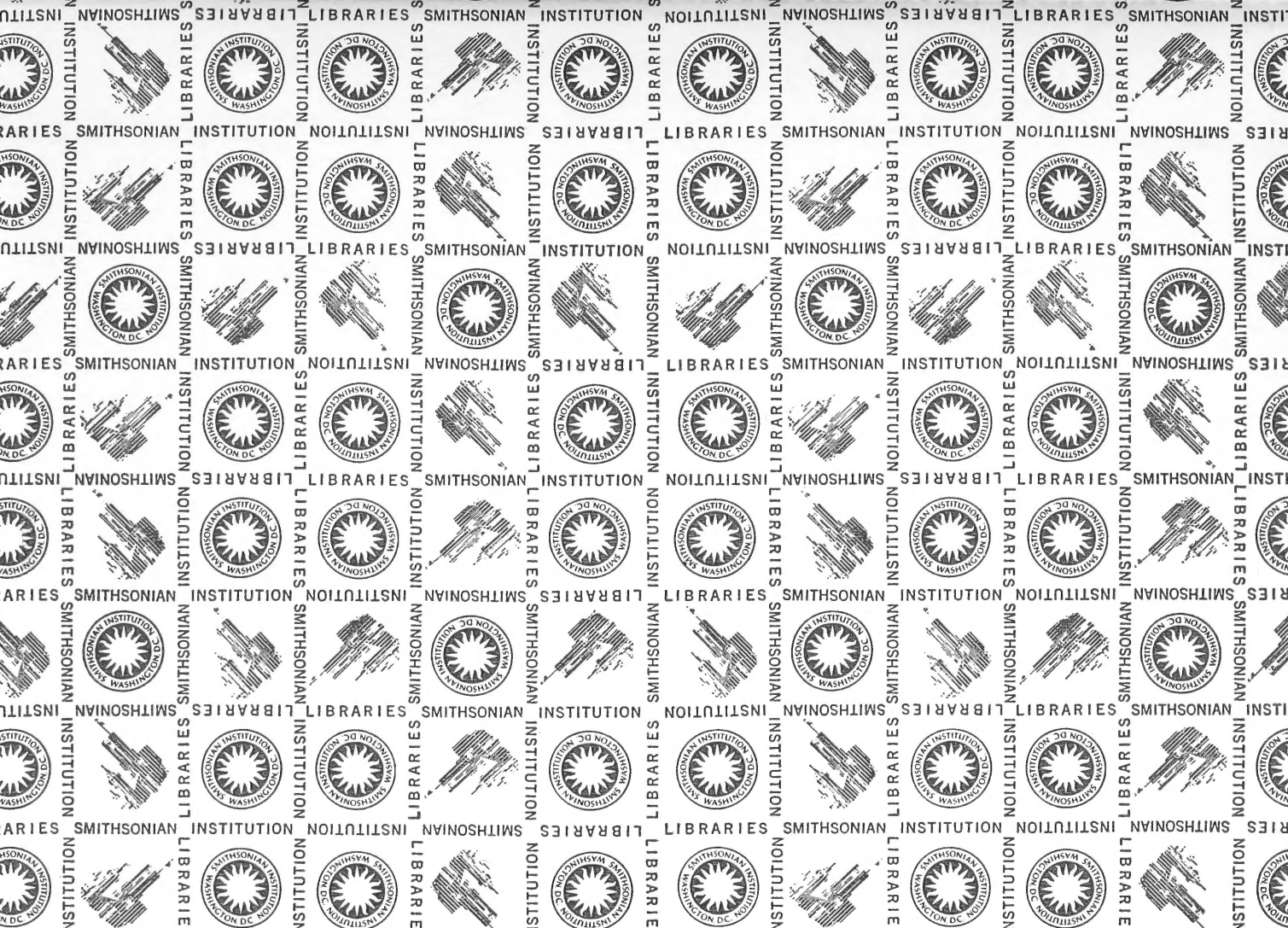
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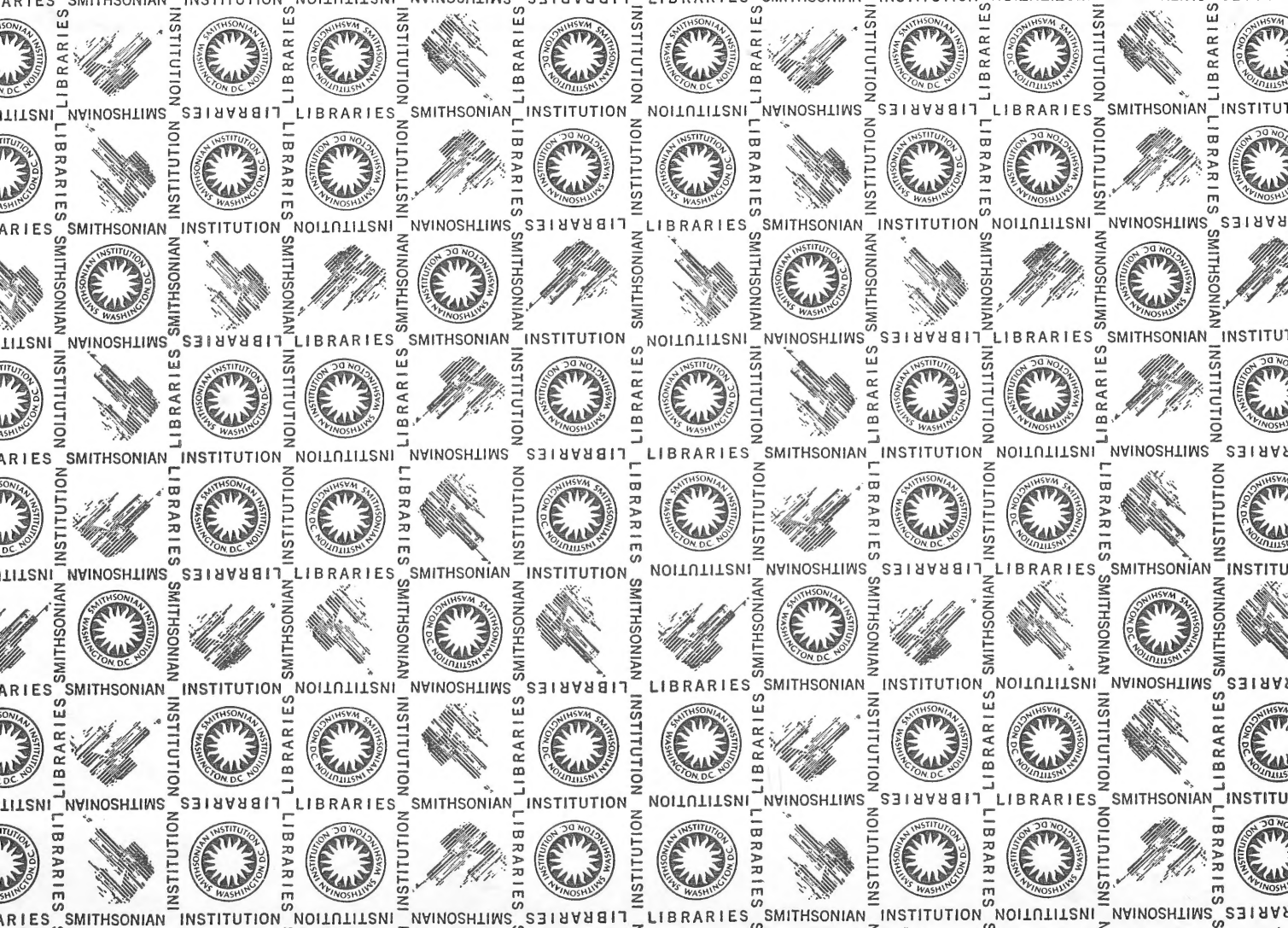
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